SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES

SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION LIBRARIES

PROCEEDINGS

of the

Biological Society of

Washington

VOLUME 104
1991

Vol. 104(1) published 13 March 1991
Vol. 104(2) published 18 June 1991
Vol. 104(3) published 25 September 1991
Vol. 104(4) published 18 December 1991

WASHINGTON
PRINTED FOR THE SOCIETY

EDITOR

C. Brian Robbins

ASSOCIATE EDITORS

Classical Languages
George C. Steyskal

Invertebrates
Stephen D. Cairns
Frank D. Ferrari
Rafael Lemaitre

Plants
David B. Lellinger

Vertebrates
G. David Johnson

Insects
Wayne N. Mathis

All correspondence should be addressed to the
Biological Society of Washington, Smithsonian Institution
Washington, D.C. 20560

Allen Press Inc.
Lawrence, Kansas 66044

OFFICERS AND COUNCIL
of the
BIOLOGICAL SOCIETY OF WASHINGTON
FOR 1990–1991

OFFICERS

President
LESLIE W. KNAPP

President-Elect
STORRS L. OLSON

Secretary
G. DAVID JOHNSON

Treasurer
MICHAEL VECCHIONE

COUNCIL

Elected Members

ROGER F. CRESSEY, JR.
JANET R. GOMON
ROBERT HERSHLER
JANET W. REID
WAYNE C. STARNES
JEFFERY T. WILLIAMS

TABLE OF CONTENTS

Volume 104

Alvarez, Fernando and José Luis Villalobos. A new genus and two new species of freshwater crabs from México, *Odontothelphusa toninae* and *Stygothelphusa lopez-formenti* (Crustacea: Brachyura: Pseudothelphusidae) 288–294

Anderson, William D., Jr. and John E. Randall. A new species of the anthiine genus *Plectranthias* (Pisces: Serranidae) from the Sala Y Gómez Ridge in the eastern South Pacific, with comments on *P. exsul* 335–343

Aoki, Masakuzu. A new species of caprellid associated with hydroids from southern Japan (Crustacea: Amphipoda: Caprellidae) 91–95

Asakura, Akira. A new hermit crab (Decapoda: Paguridae) from rocky shores of the Ogasawara (Bonin) Islands 793–799

Ascorra, César F., Don E. Wilson, and Alfred L. Gardner. Geographic distribution of *Micronycteris schmidtorum* Sanborn (Chiroptera: Phyllostomidae) 351–355

Baba, Keiji and Enrique Macpherson. Reexamination of the type material of *Munida militaris* Henderson, 1885 (Crustacea: Decapoda: Galatheidae), with the selection of a lectotype 538–544

Blake, James A. A new species of *Hesiocaeca* (Polychaeta: Hesionidae) from hydrothermal vents at the Mariana back-arc basin with notes on other polychaetes 175–180

Bowman, Thomas E. and Thomas M. Iliffe. *Annina fustis,* a new isopod from Phang Nga, Thailand (Crustacea: Isopoda: Cirolanidae) 247–252

Brooks, Daniel R., Eric P. Hoberg, and Peter J. Weekes. Preliminary phylogenetic systematic analysis of the major lineages of the Eucestoda (Platyhelminthes: Cercomeria) 651–668

Brusca, Richard C. and Hans-Georg Müller. *Skuphonura kensleyi* (Crustacea: Isopoda), a new anthuridean species from the Caribbean coast of Colombia 593–602

Cairns, Stephen D. New records of Stylasteridae (Hydrozoa: Hydroida) from the Galápagos and Cocos Islands 209–228

Carleton, Michael D. and Christine Martinez. Morphometric differentiation among West African populations of the rodent genus *Dasymys* (Muroidea: Murinae), and its taxonomic implications 419–435

Chan, Tin-Yam and Hsiang-Ping Yu. Two similar species: *Plesionika edwardsii* (Brandt, 1851) and *Plesionika crosnieri,* new species (Crustacea: Decapoda: Pandalidae) 545–555

Child, C. Allan. Pycnogonida of the western Pacific islands, IX. A shallow-water Guam survey, 1984 138–146

Coleman, C. O. and J. L. Barnard. Redescription of two species of *Pseudiphimediella* from the Southern Ocean (Amphipoda: Iphimediidae) 76–90

Coleman, C. O. and J. L. Barnard. Revision of Iphimediidae and similar families (Amphipoda: Gammariidea) 253–268

Coleman, C. O. and J. L. Barnard. *Curidia magellanica,* new species, from Magellan Strait (Crustacea: Amphipoda: Ochlesidae) 269–278

Coleman, C. O. and J. L. Barnard. *Amatiquakius forsberghi,* a new genus and species from Alaska (marine Amphipoda: Epimeriidae) 279–287

Collette, Bruce B., David G. Smith, and Eugenia B. Böhlke. *Gymnothorax parini,* a new species of Moray Eel (Teleostei: Muraenidae) from Walters Shoals, Madagascar Ridge 344–350

Curini-Galletti, Marco C. Monocelididae (Platyhelminthes: Proseriata) from Puerto Rico. I. Genera *Minona* and *Monocelis* 229–240

Decker, Denise M. Systematics of the coatis, genus *Nasua* (Mammalia: Procyonidae) 370–386

Dojiri, Masahiro and Robert A. Brantley. *Lepeophtheirus spatha,* a new species of copepod (Siphonostomatoida: Caligidae) parasitic on the California halibut from Santa Monica Bay, California 727–735

Erséus, Christer. Records of the marine genus *Bathydrillus* (Oligochaeta: Tubificidae) from California, with descriptions of two new species 622–626

Erséus, Christer. Two new deep-water species of the gutless genus *Olavius* (Oligochaeta: Tubificidae) from both sides of North America 627–630
Flint, Oliver S., Jr. and Luis Reyes A. Studies of Neotropical caddisflies, XLVI: The Trichoptera of the Río Moche basin, Department of La Libertad, Peru 474–492
Formas, J. Ramón. The karyotypes of the Chilean frogs *Eupsophus emiliopugnini* and *E. vertebralis* (Amphibia: Anura: Leptodactylidae) 7–12
Glasby, Christopher J. and Kristian Fauchald. Redescription of *Helmetophorus rankini* Hartman, 1978 (Polychaeta: Helmetophoridae) and its transfer to the Flabelligeridae 684–687
Grygier, Mark J. V. L. Wagin's collections of Dendrogastridae (Crustacea: Ascothoracida) in the U.S.S.R., with designations of lectotypes 742–750
Heaney, Lawrence R., Pedro C. Gonzales, Ruth C. B. Utzurrum, and Eric A. Rickart. The mammals of Catanduanes Island: Implications for the biogeography of small land-bridge islands in the Philippines 399–415
Heard, Richard W. and Stephen Spotte. Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) of the northwest Atlantic. II. *Periclimenes patae,* new species, a gorgonian associate from shallow reef areas off the Turks and Caicos Islands and Florida Keys 40–48
Heyer, W. Ronald and Laura M. Hardy. A new species of frog of the *Eleutherodactylus lacrimosus* assembly from Amazonia, South America (Amphibia: Anura: Leptodactylidae) 436–447
Higgins, Robert P. *Pycnophyes chukchiensis,* a new homalorhagid kinorhynch from the Arctic Sea 184–188
Hobbs, Horton H., Jr. *Procambarus* (*Girardiella*) *steigmani,* a new crayfish (Decapoda: Cambaridae) from a long-grass prairie in northeastern Texas 309–316
Hobbs, Horton H., Jr. A new generic assignment for a South American crayfish (Decapoda: Parastacidae) with revised diagnoses of the South American genera and comments on the parastacid mandible 800–811
Hobbs, Horton H., Jr. and Richard Franz. A new troglobitic crayfish, *Procambarus* (*Lonnbergius*) *morrisi,* (Decapoda: Cambaridae) from Florida 55–63
Hobbs, Horton H., Jr. and Daniel J. Peters. Additional records of entocytherid Ostracods infesting burrowing crayfishes, with descriptions of five new species 64–75
Hobbs, H. H., III. A new pseudothelphusid crab from a cave in southern Costa Rica (Decapoda: Brachyura) 295–298
Hulsemann, Kuni. *Calanus euxinus,* new name, a replacement name for *Calanus ponticus* Karavaev, 1894 (Copepoda: Calanoida) 620–621
Humes, Arthur G. Copepoda associated with the scleractinian coral genus *Montipora* in the Indo-Pacific 101–137
Kennedy, George L. and Howard E. Schorn. Annotated catalogue of California Tertiary paleobotanical types transfered to University of California of Paleontology 1–6
Kensley, Brian and Richard W. Heard. An examination of the shrimp family Callianideidae (Crustacea: Decapoda: Thalassinidea) 493–537
Knapp, Leslie W. *Platycephalus chauliodous,* a new flathead fish from the eastern Indian Ocean (Teleostei: Platycephalidae) 23–30
Leal, José H. *Arene boucheti,* a new intertidal liotiine turbinid (Mollusca: Gastropoda: Trochoidea) from Trinidade Island, South Atlantic Ocean 241–246
Lundberg, John G., Francisco Mago-Leccia, and Pedro Nass. *Exallodontus aguanai,* a new genus and species of Pimelodidae (Pisces: Siluriformes) from deep river channels of South America, and delimitation of the subfamily Pimelodinae 840–869
Manning, Raymond B. and Darryl L. Felder. Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea) 764–792
Manning, Raymond B. and C. W. Hart, Jr. A new species of *Processa* from Bermuda (Crustacea: Decapoda: Caridea) 317–321
Martin, Joel W. and Bernard Ormsby. A large brachyuran-like larva of the Hippidae (Crustacea: Decapoda: Anomura) from the Banda Sea, Indonesia: the largest known zoea 561–568
Mathis, Wayne N. and James F. Edmiston. S. W. Williston's species of Ephydridae (Diptera) from St. Vincent (West Indies) 816–839

Miura, Tomoyuki and Jun Hashimoto. *Nicomache ohtai,* new species (Polychaeta: Maldanidae) collected from the Hatsushima cold-seep in Sagami Bay 159–165
Miura, Tomoyuki and Jun Hashimoto. Two new branchiate scale-worms (Polynoidae: Polychaeta) from the hydrothermal vent of the Okinawa trough and the volcanic seamount off Chichijima Island 166–174
Modlin, Richard F. *Paranebalia belizensis,* a new species from shallow waters off Belize, Central America (Crustacea: Malacostraca: Leptostraca) 603–612
Munroe, Thomas A., Martha S. Nizinski, and M. N. Mahadeva. *Symphurus prolatinaris,* a new species of shallow-water tonguefish (Pleuronectiformes: Cynoglossidae) from the eastern Pacific 448–458
Ormsby, Bernard. *Synisoma wetzerae,* a new species and the first record of *Synisoma* from the New World (Crustacea: Isopoda: Valvifera: Idoteidae) 758–763
Parin, N. V. Three new species of the bentho-pelagic fish genus *Plagiogeneion* from the southern Pacific and Indian Oceans (Teleostei: Emmelichthyidae) 459–467
Petit, Richard E. and M. G. Harasewych. A new *Admetula* (Gastropoda: Cancellariidae) from South Africa 181–183
Pettibone, Marian H. Polynoids commensal with gorgonian and stylasterid corals, with a new genus, new combinations, and new species (Polychaeta: Polynoidae: Polynoinae) 688–713
Pettibone, Marian H. Polynoid Polychaetes commensal with antipatharian corals 714–726
Poss, Stuart G. and G. David Johnson. *Matsubarichthys inusitatus,* a new genus and species of velvetfish (Scorpaeniformes: Aploactinidae) from the Great Barrier Reef 468–473
Reid, Janet W. The Stillman Wright collection of Copepoda (Crustacea) from South America in the National Museum of Natural History, Smithsonian Institution 736–741
Rice, A. L. and J. E. Miller. Chirostylid and galatheid crustacean associates of coelenterates and echinoderms collected from the *Johnson-Sea-Link* submersible, including a new species of *Gastroptychus* 299–308
Rickart, Eric A. and Lawrence R. Heaney. A new species of *Chrotomys* (Rodentia: Muridae) from Luzon Island, Philippines 387–398
Rodriguez, Sergio de Almeida and Brian Kensley. *Eutrichocheles pindatyba,* a new axiid shrimp (Crustacea: Decapoda: Thalassinidea) from Brazil 556–560
Romero, Raúl Castro and Hernán Baeza Kuroki. A scanning electron microscope study of the buccal complex of *Metapeniculus antofagastensis* (Copepoda: Pennellidae) 613–619
Rosenblatt, Richard H. and G. David Johnson. *Parmops coruscans,* a new genus and species of Flashlight Fish (Beryciformes: Anomalopidae) from the South Pacific 328–334
Sakai, Katsushi. On *Paracalocaris sagamiensis,* a new genus and species from Japan (Decapoda: Thalassinidea: Axiidae) 30–39
Solís-Weiss, Vivianne and Luis Espinasa P. *Lycastilla cavernicola,* a new freshwater nereidid from an inland Mexican cave (Polychaeta: Nereididae: Namanereidinae) 631–639
Solís-Weiss, Vivianne, Kristian Fauchald, and Arno Blankensteyn. Trichobranchidae (Polychaeta) from shallow warm water areas in the western Atlantic Ocean 147–158
Spangler, Paul J. and Robin A. Faitoute. A new genus and species of neotropical water beetle, *Jolyelmis auyana,* from a Venezuelan Tepui (Coleoptera: Elmidae) 322–327
Steadman, David W. The identity and taxonomic status of *Megapodius stairi* and *M. burnabyi* (Aves: Megapodiidae) 870–877
Sterrer, Wolfgang. *Triplignathia adriatica,* new genus and species, and a typology of mouth parts in Austrognathiidae (Gnathostomulida) 640–646
Thomas, James Darwin and J. L. Barnard. *Photis trapherus,* a new elephantine species from the Caribbean Sea (Crustacea: Amphipoda) 96–100
Thomas, James Darwin and J. L. Barnard. Two new species of *Netamelita* from the Caribbean Sea (Crustacea: Amphipoda: Gammaridae) 583–592
Thompson, Fred G. and Robert Hershler. New hydrobiid snails (Mollusca: Gastropoda: Prosobranchia: Runcatelloidea) from North America 667–681
Tyler, James C. and Colin Patterson. The skull of the Eocene *Triodon antiquus* (Tridontidae: Tetraodontiformes): similar to that of the Recent threetooth pufferfish *T. macropterus* 878–891
Vari, Richard P. and Sandra J. Raredon. The genus *Schizodon* (Teleostei: Ostariophysi: Anostomidae) in Venezuela, a reappraisal 12–22

Watling, Les. Rediagnosis and revision of some Nannastacidae (Crustacea: Cumacea).. 751–757
Watson, George E., Storrs L. Olson, and J. Robert Miller. A new subspecies of the Double-crested Cormorrant, *Phalacrocorax auritus,* from San Salvador, Bahama Islands..... 356–369
Weerdt, Walentina H. de, Klaus Rützler, and Kathleen P. Smith. The Chalinidae (Porifera) of Twin Cays, Belize, and adjacent waters..... 189–205
Wicksten, Mary K. *Pandalus gurneyi* Stimpson synomymized with *Pandalus danae* Stimpson (Decapoda: Pandalidae)..... 812–815
Williams, Austin B. and Richard W. Heard. *Upogebia spinistipula,* a new burrowing shrimp from the Florida shelf, northeastern Gulf of Mexico (Decapoda: Thalassinidea: Upogebiidae)..... 49–54
Williams, Austin B. and Robert B. Moffitt. Crabs from the Mariana Archipelago: *Bothromaia griffini* new genus and species (Brachyura, Majidae), and notes on *Poupinia hirsuta* Guinot (Homoloidea, Popiniidae)..... 569–582

INDEX TO NEW TAXA

Volume 104

(New taxa are indicated in *italics*; new combinatiosn designated n.c.)

PORIFERA

Demospongea

Haliclona *magnifica* 194
mucifibrosa 190
pseudomolitba 197
twincayensis 196
tubifera n.c. 200

COELENTERATA

Hydrozoa

Lepidopora *concatenata* 211
Pliobothrus *fistulosus* 214
Stylaster *cocosensis* 220

PLATYHELMINTHES

Minona *paulmartensi* 231
puertoricana 230
Monocelis *alboguttata* 235

GNATHOSTOMULIDA

Triplignathia 640
adriatica 641

KINORHYNCHA

Pycnophyes *chukchiensis* 185

MOLLUSCA

Gastropoda

Admetula *epula* 181
Arene *boucheti* 241
Aroapyrgus *polius* 669
Cochliopa *perforata* 671
Heleobops *clytus* 672
torquatus 674
Lithococcus *aletes* 676
Littoridina *microcona* 677
Mesobia 678
pristina 679
Texapyrgus 680
longleyi 681

ANNELIDA

Polychaeta

Antipathipolyeunoa 715
nuttingi 716
Bayerpolynoe 719
floridensis 719

Branchipolynoe *pettiboneae* ... 166
Gorgoniapolynoe ... 688
bayeri ... 690
caeciliae n.c. ... 704
cairnsi ... 693
corralophila n.c. ... 709
galapagensis ... 698
guadalupensis ... 700
muzikae ... 695
pelagica ... 712
uschakovi n.c. ... 700
Hesiocaeca *hessleri* ... 175
Lycastilla ... 632
cavernicola ... 632
Nicomache *ohtai* ... 159
Opisthotrochopodus *japonicus* ... 169
Terebellides *carmenensis* ... 151
lanai ... 153
parvus ... 152
Tottonpolynoe ... 722
symantipathicola ... 722

ARTHROPODA

Pycnogonida

Anoplodactylus tenuicorpus n.c. ... 142
Eurycyde *sertula* ... 139

Crustacea

ACANTHONOTOZOMELLIDAE ... 257
Amatiquakius ... 279
forsberghi ... 280
ANACALLIINAE ... 786
Ankylocythere *prolata* ... 64
Annina *fustis* ... 247
Bathydrilus *parkeri* ... 623
rusticus ... 624
Biffarius ... 769
Bothromaia ... 569
griffini ... 570
Calanus *euxinus* new name ... 621
CALLIANOPSINAE ... 787
CALLICHIRINAE ... 775
Caprella *glabra* ... 91
CHERAMINAE ... 780
Crosniera ... 500
CTENOCHELIDAE ... 784
CTENOCHELINAE ... 784
Cumella (C.) hirsuta n.c. ... 752
Curidia *magellanica* ... 272
Cyclaspocumella new subgenus ... 753
Dactylocythere *guyandottae* ... 68
lepta ... 68
pygidion ... 70
Dawsonius ... 785
DIKWIDAE ... 260
Elassocumella ... 753
Eucalliax ... 781
EUCALLIINAE ... 781

Euryte *bellatula* 102
Eutrichocheles *pindatyba* 556
Gastroptychus salvadori 299
Haplomolgus *incolumis* 107
Hetairosyna 113
laciniata 119
sororia 124
terpna 113
Lepeophtheirus *spatha* 727
Marcusiaxius *colpos* 506
Meticonaxius *bouvieri* 512
Michelea 519
lamellosa 519
pillsburyi 522
Mictaxius 527
thalassicola 527
Neotrypaea 771
Netamelita *brocha* 585
tabaci 589
Notiax 772
ODIIDAE 262
Odontothelphusa *toninae* 288
Olavius *rallus* 629
tannerensis 627
Pagurus *insulae* 793
Paracalocaris 30
sagamiensis 31
Paranebalia *belizensis* 603
Periclimenes *patae* 40
Photis *trapherus* 96
Plectocythere *kentuckiensis* 72
Plesionika *crosnieri* 546
Procambarus (Girardiella) *steigmani* 309
Procambarus (Lonnbergius) *morrisi* 56
Processa *famelica* 317
Pseudothelphusa *puntarenas* 295
Scherocumella 754
brachydactyla n.c. 754
clavata n.c. 754
gurneyi n.c. 754
japonica n.c. 754
leptura n.c. 754
nasuta n.c. 754
nichollsi n.c. 754
pilgrimi n.c. 754
sheardi n.c. 754
stephenseni n.c. 754
vieta n.c. 754
Schizocuma calmani n.c. 755
divisa n.c. 755
molossa n.c. 755
spinoculata n.c. 755
spinosa n.c. 755
Skuphonura *kensleyi* 594
Stygothelphusa 290
lopezformenti 291
Synisoma *wetzerae* 758

Tychomyzon 126
petalum 128
Virilastacus 802
araucanius n.c. 802
Upogebia *spinistipula* 49

Insecta

Chimarra (Chimarra) *dolabrifera* 478
Chimarra (Curgia) *otuzcoensis* 480
Hyadina nitifrons n.c. 835
Hydroptila *sicilicula* 484
Jolyelmis 322
auyana 325
Neotrichia *riparia* 486
Polytrichophora desmata n.c. 826
Smicridea (Rhyacophylax) *bidactyla* 483
Triaenodes *peruanus* 488

CHORDATA

Pisces

Exallodontus 843
aguanai 847
Gymnothorax *parini* 344
Matsubarichthys 468
inusitatus 469
Parmops 328
coruscans 329
Plagiogeneion *fiolenti* 463
geminatum 460
unispina 461
Platycephalus *chauliodous* 24
Plectranthias *parini* 336
Symphurus *prolatinaris* 449

Amphibia

Eleutherodactylus *zimmermanae* 436

Aves

Phalacrocorax auritus *heuretus* 360

Mammalia

Chrotomys *gonzalesi* 389

QH
1
34X
NH

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

VOLUME 104 NUMBER 1
13 MARCH 1991
ISSN 0006-324X

THE BIOLOGICAL SOCIETY OF WASHINGTON

1990–1991

Officers

President: Leslie W. Knapp
President-elect: Storrs L. Olson
Secretary: G. David Johnson
Treasurer: Michael Vecchione

Elected Council

Roger F. Cressey, Jr.
Janet R. Gomon
Robert Hershler
Janet W. Reid
Wayne C. Starnes
Jeffery T. Williams

Custodian of Publications: Austin B. Williams

PROCEEDINGS

Editor: C. Brian Robbins

Associate Editors

Classical Languages: George C. Steyskal

Plants: David B. Lellinger
Insects: Wayne N. Mathis

Invertebrates: Stephen D. Cairns
Frank D. Ferrari
Rafael Lemaitre
Vertebrates: G. David Johnson

Membership in the Society is open to anyone who wishes to join. There are no prerequisites. Annual dues of $15.00 ($20.00 to non-USA addresses) include subscription to the *Proceedings of the Biological Society of Washington.* Library subscriptions to the *Proceedings* are: $25.00 within the U.S.A., $30.00 elsewhere.

The *Proceedings of the Biological Society of Washington* (USPS 404-750) is issued quarterly. Back issues of the *Proceedings* and the *Bulletin of the Biological Society of Washington* (issued sporadically) are available. Correspondence dealing with membership and subscriptions should be sent to The Treasurer, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Manuscripts, corrected proofs, editorial questions should be sent to the Editor, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Known office of publication: National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Printed for the Society by Allen Press, Inc., Lawrence, Kansas 66044

Second class postage paid at Washington, D.C., and additional mailing office.

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, National Museum of Natural History, Washington, D.C. 20560.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 1–6

ANNOTATED CATALOGUE OF CALIFORNIA TERTIARY PALEOBOTANICAL TYPES TRANSFERRED TO UNIVERSITY OF CALIFORNIA MUSEUM OF PALEONTOLOGY

George L. Kennedy and Howard E. Schorn

Abstract.—Most paleobotanical holdings of the Natural History Museum of Los Angeles County were transferred to the University of California Museum of Paleontology, Berkeley, in February 1990. They included 41 type, figured, or referred specimens representing 21 species of Miocene marine algae described by N. L. Gardner or by B. C. Parker and E. Y. Dawson, and seven species of Pliocene and Miocene coniferous and deciduous trees and shrubs described by D. I. Axelrod or by B. C. Templeton. Four additional type specimens could not be located and are presumed to be lost.

Most paleobotanical holdings of the Natural History Museum of Los Angeles County, Los Angeles, California (LACMNH) were transferred to the Museum of Paleontology, University of California, Berkeley, California (UCMP) in February, 1990. This relatively small collection contained 41 type, figured, or referred specimens representing 21 species of Miocene marine algae described by Gardner (1923 [1924]) or Parker & Dawson (1965) and seven species of Pliocene and Miocene coniferous and deciduous trees and shrubs described by Axelrod (1937) or by Templeton (1953). Four specimens, representing three species described by Axelrod (1937), could not be located and are presumed to be lost. Four species, three represented only by single specimens, are type species for the form genera *Julescraneia, Paleopikea, Paleosiphonia,* and *Paleothamnion* (Parker & Dawson 1965).

Not included in the transfer are the paleobotanical specimens from the upper Pleistocene asphalt deposits of Rancho La Brea, including unpublished types of Templeton (1964) that are currently housed in the George C. Page Museum of La Brea Discoveries, a satellite facility of LACMNH. Also not included is the large collection of Oligocene plants from Rott, Germany assembled by the late Georg Statz and described in a series of papers by Hermann Weyland.

Because paleobotany was never a formally recognized discipline at LACMNH, specimens have been variously labeled, and published under, one or more of the following administrative, departmental, or institutional numbering systems: Registrar loan and specimen number, Registrar Accession number, Vertebrate Paleontology specimen number (subsequently used as basis for Paleobotany catalogue series), Vertebrate Paleontology locality number, Paleobotany (PB-) catalogue number, and California Institute of Technology (CIT) Vertebrate Paleontology locality or specimen number. The catalogue series for all published numbers are identified in the following list.

Specimens cited are grouped together by division (Chlorophyta, Phaeophyta, Rhodophyta, Coniferophyta, and Magnoliophyta) and within each division are arranged alphabetically by genus and species name as originally published. Each entry includes a bibliographic reference, LACMNH type category and number as originally published (with explanations thereof), UCMP

Paleobotany type number, and remarks when needed. All inquiries concerning the examination or use of specimens should be addressed to the Museum of Paleontology, University of California, Berkeley, California 94720.

Chlorophyta

Caulerpites denticulata Parker & Dawson, 1965:276, pls. 76, 81 (fig. 5).

Holotype: "Type: LACM No. PB-1523 from site 1267." [LACMNH Paleobotany cat. no. PB-1523, Vertebrate Paleontology loc. 1267.]

=UCMP Paleobot. 10,859.

Phaeophyta

Cystoseira occidentalis Gardner, 1923 [1924]:363, unnumbered text-fig.

Holotype: [Not stated, but obviously the specimen on which the text figure is based, which is LACMNH Registrar Accession no. A.1011.]

=UCMP Paleobot. 10,860.

Remarks: The holotype was not located by Parker & Dawson (1965:283) and remained unrecognized until preparation of this catalogue. See also *Palaeohalidrys occidentalis* (Gardner) Parker & Dawson (1965).

Cystoseirites ornata Parker & Dawson, 1965: 284, pls. 80 (fig. 6), 86 (figs. 1, 2).

Holotype: "Type: LACM No. PB-1533 [pl. 80, fig. 6; pl. 86, fig. 1] from site 388." [LACMNH Paleobotany cat. no. PB-1533; CIT Vertebrate Paleontology loc. 388.]

=UCMP Paleobot. 10,861.

Paratype: "A second specimen, LACM No. PB-1534 [part (pl. 86, fig. 2) and partial counterpart] from site 388." [LACMNH Paleobotany cat. no. PB-1534; CIT Vertebrate Paleontology loc. 388.]

=UCMP Paleobot. 10,862.

Julescraneia grandicornis Parker & Dawson, 1965:278, pls. 77, 80 (fig. 3).

Holotype: "Type: LACM No. PB-1524 [pl. 77; pl. 80, fig. 3 (sketched reconstruction)] from site 1267." [LACMNH Paleobotany cat. no. PB-1524, Vertebrate Paleontology loc. 1267.]

=UCMP Paleobot. 10,863.

Referred specimen: "Impression of a brown-algal blade (PB-1546) which may represent a fragment of the blade of *Julescraneia.*" [LACMNH Paleobotany cat. no. PB-1546, Vertebrate Paleontology loc. 1267.]

=UCMP Paleobot. 10,864.

Remarks: Type species of the form genus *Julescraneia* Parker & Dawson, 1965.

Palaeohalidrys californica Gardner, 1923 [1924]:362, pl. 25.

Figured specimen (Parker & Dawson 1965:280, pls. 78, 80 (figs. 4, 5)): "LACM No. PB-350 [pl. 78] from site 350." [LACMNH Paleobotany cat. no. 350, Registrar Accession no. A.5238.]

=UCMP Paleobot. 10,871.

Remarks: The spelling for the genus as originally proposed is *Palaeohalidrys* Gardner, 1924, which is correct and must be maintained. It is difficult to ascertain if the line drawings (pl. 80, figs. 4, 5) are accurate representations of PB-350 or are stylized reconstructions.

Palaeohalidrys dendritica Parker & Dawson, 1965:281, pl. 79, fig. 1.

Holotype: "Type: LACM No. PB-1525 [fig. 1] from site 317." [LACMNH Paleobotany cat. no. PB-1525; CIT Vertebrate Paleontology loc. 317.]

=UCMP Paleobot. 10,872.

Palaeohalidrys liguliformis Parker & Dawson, 1965:282, pl. 82.

Holotype: "Type: LACM No. PB-1527 [pl. 82]." [LACMNH Paleobotany cat. no.

PB-1527; institutional locality number not assigned.]

=UCMP Paleobot. 10,873.

Paratype: "Another specimen, LACM No. PB-1528 [unfigured] from loc. 1894A." [LACMNH Paleobotany cat. no. PB-1528, Vertebrate Paleontology loc. 1894A.]

=UCMP Paleobot. 10,874.

Paratype: "Yet another specimen, PB-1540 [unfigured] from site 1267." [LACMNH Paleobotany cat. no. PB-1540, Vertebrate Paleontology loc. 1267.]

=UCMP Paleobot. 10,875 [PB-1540(?)].

Remarks: An unnumbered specimen that may be PB-1540 is in the collection, but was disassociated from the correct labels.

Palaeohalidrys linearis Parker & Dawson, 1965:281, pl. 93, upper and lower figs.

Holotype: "Type: LACM No. PB-1526 [consisting of three blocks, the largest (lower fig.) and a smaller contiguous one, and the counterpart (upper fig.) to the smaller piece] from site 317." [LACMNH Paleobotany cat. no. PB-1526; CIT Vertebrate Paleontology loc. 317.]

=UCMP Paleobot. 10,876.

Palaeohalidrys occidentalis (Gardner) Parker & Dawson, 1965:283, pls. 84, 91, 92 (fig. 2).

Figured specimens: "LACM No. PB-1529 [part (pl. 84, lower fig.) and partial counterpart] from site 1806, LACM No. PB-1530 [5 contiguous pieces (pl. 84, upper fig.; pl. 92, fig. 2) and counterpart to basal piece] from site 317A, and LACM No. PB-1532 [pl. 91] from unknown site." [LACMNH Paleobotany cat. nos. PB-1529, PB-1530, and PB-1532, Vertebrate Paleontology loc. 1806; CIT Vertebrate Paleontology loc. 317A.]

=UCMP Paleobot. 10,877 [PB-1529], 10,878 [PB-1530], 10,880 [PB-1532].

Referred specimen: "LACM No. PB-1531 [an unnumbered specimen not associated with any labels may be PB-1531] from site 1925." [LACMNH Paleobotany cat. no. PB-1531, Vertebrate Paleontology loc. 1925.]

=UCMP 10,879 [PB-1531(?)].

Palaeohalidrys superba Parker & Dawson, 1965:284, pls. 80 (fig. 7), 85.

Holotype: "Type: LACM No. PB-395 [figures] from site 317." [LACMNH Paleobotany cat. no. PB-395; CIT Vertebrate Paleontology loc. 317.]

=UCMP Paleobot. 10,881.

Remarks: Plate 85 is a negative print of the specimen.

Paleocystophora acuminata Parker & Dawson, 1965:285, pl. 87.

Holotype: "Type: LACM No. PB-1535 [pl. 87] from site 1267." [LACMNH Paleobotany cat. no. PB-1535, Vertebrate Paleontology loc. 1267.]

=UCMP Paleobot. 10,865.

Paratype: "A second specimen from the same site, LACM No. PB-1536 [unfigured]." [LACMNH Paleobotany cat. no. PB-1536, Vertebrate Paleontology loc. 1267.]

=UCMP Paleobot. 10,866.

Paleocystophora delicatula Parker & Dawson, 1965:286, pl. 79, fig. 2.

Holotype: "Type: LACM No. PB-1537 [part (fig. 2) and counterpart] from site 1925." [LACMNH Paleobotany cat. no. PB-1537, Vertebrate Paleontology loc. 1925.]

=UCMP Paleobot. 10,867.

Paleocystophora lacerodentata Parker & Dawson, 1965:286, pl. 88.

Holotype: "Type: LACM No. PB-1538 [part (pl. 88) and counterpart] from site 1879." [LACMNH Paleobotany cat. no. PB-1538, Vertebrate Paleontology loc. 1879.]

=UCMP Paleobot. 10,868.

Paleocystophora plumosa Parker & Dawson, 1965:286, pls. 81 (fig. 2), 89.

Holotype: "Type: LACM No. PB-1539 [figures] from site 1267." [LACMNH Pa-

leobotany cat. no. PB-1539, Vertebrate Paleontology loc. 1267.]
=UCMP Paleobot. 10,869.

Paleocystophora subopposita Parker & Dawson, 1965:287, pl. 90.

Holotype: "Type: LACM No. PB-365 [pl. 90] from site 365." [LACMNH Paleobotany cat. no. PB-365.]
=UCMP Paleobot. 10,870.

Rhodophyta

Chondrides flexilis Parker & Dawson, 1965: 289, pls. 92 (fig. 1), 95.

Holotype: "Type: LACM No. PB-1235 [figures] from site 1040." [LACMNH Paleobotany cat. no. PB-1235, Vertebrate Paleontology loc. 1040.]
=UCMP Paleobot. 10,882.

Chondrides ramulosa Parker & Dawson, 1965:291, pl. 96, fig. 1.

Holotype: "Type: LACM No. PB-1545 [fig. 1] from site EDM-4." [LACMNH Paleobotany cat. no. PB-1545; E. D. Mitchell locality 4.]
=UCMP Paleobot. 10,883.

Chondrides recurva Parker & Dawson, 1965: 289, pls. 81 (fig. 6), 94 (fig. 2).

Holotype: "Type: LACM No. PB-1542 [2 branches ("specimens"), part (figs. 6, 2) and counterpart], probably from site 317." [LACMNH Paleobotany cat. no. PB-1542; CIT Vertebrate Paleontology loc. 317 (?).]
=UCMP Paleobot. 10,884.

Delesserites acuminata Parker & Dawson, 1965:290, pl. 92, figs. 3–5.

Holotype: "Type: LACM No. PB-1544." [LACMNH Paleobotany cat. no. PB-1544.]
=UCMP Paleobot. 10,885.
Remarks: Figures 3–5 are "reconstructions from the type materials of *Delesserites acuminata.*"

Paleopikea cranei Parker & Dawson, 1965: 288, pls. 81 (fig. 4), 96 (fig. 2).

Holotype: "Type: LACM No. PB-1541 [figs. 4, 2] from site 1925." [LACMNH Paleobotany cat. no. PB-1541, Vertebrate Paleontology loc. 1925.]
=UCMP Paleobot. 10,886.
Remarks: Type species of the form genus *Paleopikea* Parker & Dawson, 1965.

Paleosiphonia oppositiclada Parker & Dawson, 1965:288, pls. 81 (fig. 3), 94 (fig. 1).

Holotype: "Type: LACM 10,202 [part (figs. 3, 1) and counterpart]." [LACMNH Paleobotany cat. no. PB-2990; CIT Vertebrate Paleontology loc. 387B.]
=UCMP Paleobot. 10,887.
Remarks: The specimen number "LACM 10,202" cited in Parker & Dawson (1965: 288) is a CIT Vertebrate Paleontology specimen number for *Bathylagus angelensis,* one of two fish on the block of diatomite with *P. oppositiclada.* This is the type species of the form genus *Paleosiphonia* Parker & Dawson, 1965.

Paleothamnion acicularis Parker & Dawson, 1965:290, pl. 96, fig. 3.

Holotype: "Type: LACM No. PB-1543 [fig. 3] from site 1925." [LACMNH Paleobotany cat. no. PB-1543, Vertebrate Paleontology loc. 1925.]
=UCMP Paleobot. 10,888.
Remarks: Type species of the form genus *Paleothamnion* Parker & Dawson, 1965.

Coniferophyta

Pinus hazeni Axelrod, 1937:165, pl. 2, fig. 4.

Paratype: "$\frac{1014}{719}$ [unfigured]." [LACMNH Paleobotany cat. no. PB-719, Vertebrate paleontology loc. 1014 (sublocality 1).]

=UCMP Paleobot. 10,889.

Remarks: The holotype and only other original specimen is UCMP Paleobot. 958 (fig. 4). Two additional specimens subsequently figured by Axelrod (1986:625, figs. 75, 76) are cited erroneously as paratypes, but were not part of the original material studied by Axelrod (1937).

Pinus lawsoniana Axelrod, 1967.

See Remarks under *Pinus pretuberculata* Axelrod, 1937.

Pinus paucisquamosa Templeton, 1953:64, pl. 11, figs. 1, 2, 3b.

Holotype: "Type, Paleobotany No. 1400 [fig. 1]," and "4432/PB-1400." [LACMNH Paleobotany cat. no. PB-1400, Registrar Accession no. A.4432.]

=UCMP Paleobot. 10,890.

Remarks: Templeton (1953:figs. 2, 3b) as well as Axelrod (1986:fig. 46) also figured latex(?) casts made from the holotype mold.

Pinus pretuberculata Axelrod, 1937:166, pl. 3, figs. 3, 4.

Syntypes: "Cotypes, L.$\frac{1306}{1014}$ [fig. 3; missing], $\frac{1014}{696}$ [fig. 4; missing]." [LACMNH Registrar Loan no. L.1306, Vertebrate Paleontology loc. 1014 (sublocalities 1 [PB-696] and 3 [PB-688]), Paleobotany cat. nos. PB-688 and PB-696.]

=UCMP Paleobot. 10,891 [PB-688; missing], 10,892 [PB-696; missing]; UCMP numbers assigned in absentia.

Remarks: *Pinus pretuberculata* was described on the basis of two specimens, both of which are missing and presumed lost. Specimen 688 (=PB-688) belonged to Mr. D. G. Wolfskill of Beaumont, California, and was on loan to LACMNH when it was in turn loaned to R. W. Chaney (UCMP) in 1933. The specimen was returned to the Museum in 1936, and appears to have been returned to its owner. A search of the Museum Registrar's records failed to uncover any paperwork that would suggest that the Museum ever acquired this specimen. Axelrod (1967:115–116) has since referred this specimen to *P. lawsoniana* Axelrod, 1967.

Specimen 696 (=PB-696) was also returned to the Museum in 1936 and was one of several of Axelrod's (1937) type specimens from the Mount Eden flora that were placed on exhibit in 1947. An original label for PB-696 was found among the specimens that had been taken off display, but it was not associated with the figured syntype. A search for the specimen was made, but it could not be located and is presumed to be lost. This specimen was cited as the "holotype" by Axelrod (1967:124), and subsequently designated as the lectotype (Axelrod 1986:631).

Pseudotsuga premacrocarpa Axelrod, 1937:167, pl. 3, figs. 1, 2.

Syntypes: "Cotypes, L.$\frac{1313}{6}$ [unfigured], $\frac{1014}{749}$ [unfigured]." [LACMNH Registrar Loan no. L.1313 (specimen 6), Vertebrate Paleontology loc. 1014 (sublocality 6a), Paleobotany cat. no. PB-749.]

=UCMP Paleobot. 10,893 [L.1313/6], 10,894 [PB-749].

Remarks: The remaining three syntypes are UCMP Paleobot. 962 (fig. 2), 963 (fig. 1), and 964.

Magnoliophyta

Juglans beaumontii Axelrod, 1937:171, pl. 4, figs. 11, 12.

Syntypes: "Cotypes, L.$\frac{1313}{103}$ [unfigured], L.$\frac{1313}{127}$ [unfigured], $\frac{1014}{1}$ [fig. 12; missing]." [LACMNH Registrar Loan no. L.1313 (specimens 103 & 127), Vertebrate Paleontology loc. 1014 (sublocality 1).]

=UCMP Paleobot. 10,895 [L.1313/103],

10,896 [L.1313/127], 10,897 [1014/1; missing, UCMP number assigned in absentia].

Remarks: The original label for specimen 1014/1 is present, but was not associated with the figured syntype, which is missing. The remaining syntypes are UCMP Paleobot. 971 (fig. 11) and 972.

Prunus preandersonii Axelrod, 1937:176, pl. 4, figs. 9, 10.

Syntypes: "Cotypes, L.$\frac{1313}{94}$ [fig. 9], L.$\frac{1313}{100}$ [fig. 10], L.$\frac{1313}{112}$ [unfigured]." [LACMNH Registrar Loan no. L.1313 (specimens 94, 100, & 112).]

=UCMP Paleobot. 10,898 [L.1313/94], 10,899 [L.1313/100], 10,900 [L.1313/112].

Prunus prefremontii Axelrod, 1937:176, pl. 4, figs. 5, 6.

Syntypes: "Cotypes, $\frac{1014}{822}$ and L.$\frac{1014}{822}$ [fig. 5], $\frac{1014}{909}$ [unfigured, missing], $\frac{1014}{912}$ and L.$\frac{1014}{912}$ [fig. 6]." [LACMNH Vertebrate Paleontology loc. 1014 (and sublocality 1 [PB-822]), Paleobotany cat. nos. PB-822, PB-909, and PB-912.]

=UCMP Paleobot. 10,901 [PB-822], 10,902 [PB-909; missing, UCMP number assigned in absentia], 10,903 [PB-912].

Literature Cited

Axelrod, D. I. 1937. A Pliocene flora from the Mount Eden Beds, southern California.—Carnegie Institution of Washington Publication 476:125–183, fig. 1, pls. 1–6.

———. 1967. Evolution of the Californian closed-cone pine forest. Pp. 93–149, figs. 1–2, pls. 1–8 *in* R. N. Philbrick, ed., Proceedings of the Symposium on the Biology of the California Islands, Santa Barbara Botanic Garden, Santa Barbara.

———. 1986. Cenozoic history of some western American pines.—Annals of the Missouri Botanical Garden 73(3):565–641, text-figs. 1–26, figs. 1–108.

Gardner, N. L. 1923 [1924]. Two new fossil algae from the Miocene.—Proceedings of the Academy of Natural Sciences of Philadelphia 75:361–363, 1 text-fig., pl. 25. [19 February 1924]

Parker, B. C., & E. Y. Dawson. 1965. Non-calcareous algae from California Miocene deposits.—Nova Hedwigia 10(1+2):273–295, pls. 76–96.

Templeton, B. C. 1953. A new record of pine cone for the Miocene epoch.—Bulletin of the Southern California Academy of Sciences 52(2):64–66, pl. 11.

———. 1964. The fruits and seeds of the Rancho La Brea Pleistocene deposits. Unpublished Ph.D. dissertation, Oregon State University, Corvallis, 224 pp.

(GLK) Earth Sciences Division, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007; (HES) Museum of Paleontology, University of California, Berkeley, California 94720.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 7–11

THE KARYOTYPES OF THE CHILEAN FROGS *EUPSOPHUS EMILIOPUGINI* AND *E. VERTEBRALIS* (AMPHIBIA: ANURA: LEPTODACTYLIDAE)

J. Ramón Formas

Abstract.—The karyotypes of *Eupsophus emiliopugini* and *E. vertebralis* are described. Both species have 28 chromosomes, and *E. vertebralis* has a telocentric chromosome which is absent in *E. emiliopugini.* Two hypotheses about the karyological evolution of these frogs are proposed.

Eupsophus emiliopugini and *E. vertebralis* are endemic and allopatric frogs of the temperate *Nothofagus* forests of southern Chile (Formas 1989a). Bogart (1970) described the chromosomes of *E. vertebralis* based on two males collected at Mehuín (Valdivia Province), and pointed out that this species has 28 chromosomes, no detected secondary constrictions and a large telocentric (t) chromosome 3. *Eupsophus vertebralis* was considered by Donoso-Barros (1976) a synonym of *E. vittatus* (Philippi, 1902), however Formas (1989b) demonstrated that *E. vittatus* is a member of the genus *Alsodes* and *E. vertebralis* is a distinct species. *Alsodes vittatus* and *E. vertebralis* are allopatric species.

This paper describes the karyotype of *E. emiliopugini* and re-describes the karyotype of *E. vertebralis.* Two hypotheses are proposed to explain the karyological evolution of both species.

Methods and Materials

Specimens of *E. emiliopugini* were collected in Puntra (Chiloé Province) and *E. vertebralis* in Mehuín (Valdivia Province), the same locality where the specimens of *E. vertebralis* karyotyped by Bogart (1970) were collected. The numbers of individuals from each locality were: Puntra (42°7′S; 73°49′W) 4 males (IZUA 2058–2061) and 2 females (IZUA 2062–2063) and Mehuín (39°26′S; 73°10′W) 9 males (IZUA 1972–1979, 1983) and 1 female (IZUA 1981). All frogs were injected with 0.3 ml of colchicine solution (0.1%) for 12 hours, and chromosomes from intestinal cells were obtained. Fragments of intestine were hypotonically treated, fixed in acetic-alcohol (1:3), and placed in 45% acetic acid. Small fragments of tissue were squashed between two slides, dipped in liquid nitrogen, and the cover-slide was removed with a razor blade. After three days the slides were stained for 10 minutes in Sorensen's phosphate buffer (pH 6.8) containing 4% Giemsa. For karyotype analysis chromosome lengths were measured on enlarged photomicrographs of metaphase-spreads (18 mitotic plates from *E. emiliopugini* and 20 from *E. vertebralis*) and relative length and arm ratio (length of long arm/length of short arm) were calculated. The relative length of the chromosomes were determined according to Bogart (1970). The centromeric positions were determined according to Levan et al. (1964). Secondary constrictions were not included in the measurements.

Specimens and slide chromosomes were deposited in the amphibian collection of the Instituto de Zoología, Universidad Austral de Chile, Valdivia (IZUA).

Results

Eupsophus emiliopugini Formas, 1989

Examination of 18 metaphase plates from a total of 4 males and 2 females revealed a

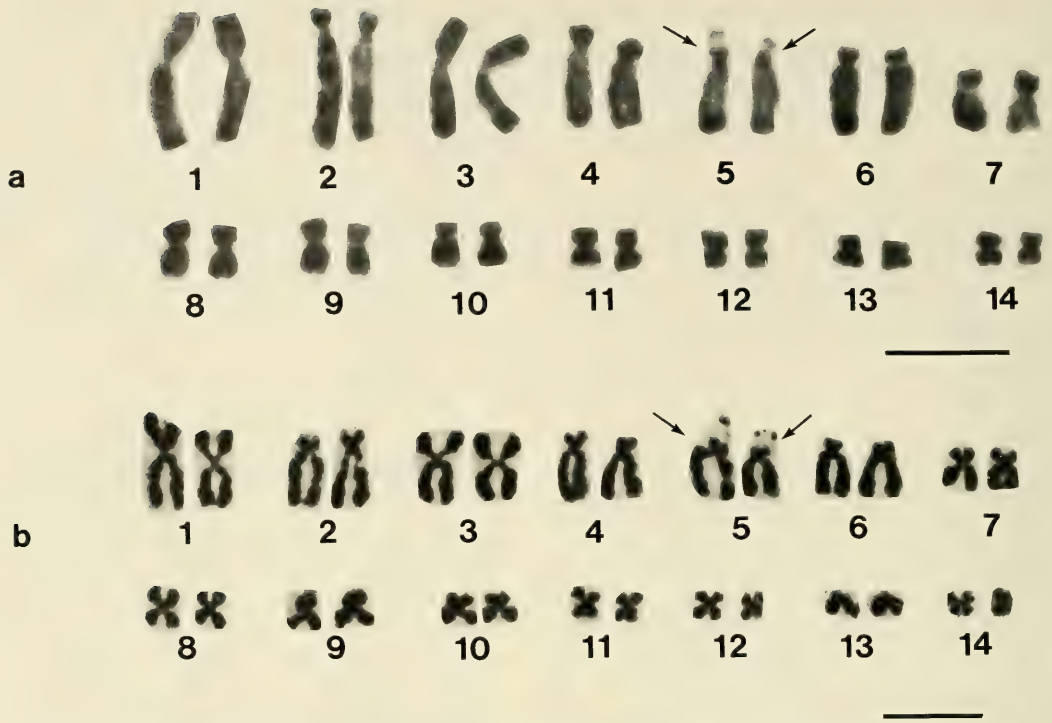


Fig. 1. Karyotypes of *Eupsophus emiliopugini* (a) and *E. vertebralis* (b). The bar indicates 10 μm.

diploid number of 2N = 28. All chromosomes are bi-armed and have a fundamental number (NF) of 56. When chromosomes are arranged in pairs of decreasing length: pairs 1–4 are large (>100 units), 5 and 6 intermediate (80–100 units), and 7–14 small (<80 units). Pairs 1, 3 and 8 through 14 are metacentric; 7 submetacentric, and 2, 4, 5 and 6 subtelocentric. The small arm of pair 5 shows an extended secondary constriction. The karyotype of *E. emiliopugini* is shown in Fig. 1a. No sexual dimorphism was detected in the karyotype. A summary of the centromeric positions and relative lengths of chromosome pairs is given in Table 1.

Eupsophus vertebralis Grandison, 1961

The karyotype of *E. vertebralis* is re-described from a total of 20 c-metaphase plates of 9 males and 1 female. The karyotype is shown in Fig. 1b. Pairs 1, 3, 8, 9, 10, 11, 12 and 14 are metacentric; 7 is submetacentric; 2, 4, 5 and 6 are subtelocentric, and pair 13 is telocentric. Pairs 1–4 are large (>100 units), 5 and 6 intermediate (80–100 units), and 7–14 small (<80 units). A summary of the centromeric positions and relative lengths of the chromosome pairs is given in Table 2. No sexual dimorphism was detected in the karyotype.

Discussion

The karyotype of *E. vertebralis* as described by Bogart (1970) differs in part when compared with the results here obtained. First, an evident secondary constriction was observed on the small arm of pair 5 (Fig. 1b). In addition, chromosome pair 3 was metacentric, not telocentric, as previously described. Finally, a telocentric not metacentric pair (13) was observed. The karyo-

Table 1.—Relative length, arm ratio (mean and standard deviations), and type of chromosomes (m = metacentric; sm = submetacentric; st = subtelocentric; t = telocentric) of *Eupsophus emiliopugini*. The number below males and females indicates the karyotypes measured. * Chromosome with secondary constriction.

	4 Males 12			2 Females 6		
Pair no.	Relative length	Arm ratio	Type	Relative length	Arm ratio	Type
1	140.81 ± 11.33	1.41 ± 0.17	m	139.90 ± 10.71	1.39 ± 0.35	m
2	122.80 ± 8.57	4.05 ± 1.44	st	122.84 ± 9.31	4.12 ± 0.94	st
3	115.24 ± 5.69	1.51 ± 0.14	m	116.01 ± 5.41	1.48 ± 0.23	m
4	107.33 ± 3.75	4.40 ± 1.38	st	108.25 ± 4.02	4.32 ± 1.12	st
5*	96.21 ± 9.21	3.60 ± 0.80	st	*96.18 ± 8.57	3.82 ± 0.79	st
6	88.27 ± 6.70	3.85 ± 0.58	st	87.93 ± 5.80	3.71 ± 0.23	st
7	61.34 ± 4.81	1.90 ± 0.24	sm	61.75 ± 4.92	1.98 ± 0.15	sm
8	54.30 ± 5.41	1.36 ± 0.20	m	53.83 ± 6.95	1.51 ± 0.39	m
9	47.39 ± 3.52	1.43 ± 0.22	m	46.80 ± 4.71	1.36 ± 0.79	m
10	44.23 ± 2.75	1.31 ± 0.29	m	44.61 ± 1.93	1.20 ± 0.24	m
11	36.38 ± 2.80	1.55 ± 0.28	m	35.95 ± 3.07	1.43 ± 0.15	m
12	31.01 ± 4.47	1.06 ± 0.08	m	31.24 ± 3.68	1.12 ± 0.09	m
13	26.57 ± 3.85	1.10 ± 0.20	m	26.14 ± 3.94	1.08 ± 0.14	m
14	21.35 ± 4.64	1.03 ± 0.08	m	21.21 ± 3.66	1.20 ± 0.14	m

types of *E. vertebralis* and *E. emiliopugini* differ in the morphology of pair 13, which is telocentric in *E. vertebralis* and metacentric in *E. emiliopugini*.

Menzies & Tippet (1976) and Bogart (1981) explained the chromosome evolution of some frog species (*Litoria infrafrenata* and *Eleutherodactylus planirostris*) by translocation and pericentric inversion events. In these cases, the chromosomal number remained constant, whereas the fundamental number and the morphology of the chromosomes showed differences. This situation is also seen in the karyotypes

Table 2.—Relative length, arm ratio (mean and standard deviations), and type of chromosomes (m = metacentric; sm = submetacentric; st = subtelocentric; t = telocentric) of *Eupsophus vertebralis*. The number below males and females indicates the karyotypes measured. * Chromosome with secondary constriction.

	9 Males 16			1 Female 4		
Pair no.	Relative length	Arm ratio	Type	Relative length	Arm ratio	Type
1	126.00 ± 7.72	1.46 ± 0.25	m	125.93 ± 4.42	1.52 ± 0.14	m
2	119.00 ± 6.60	4.01 ± 0.76	st	119.40 ± 2.31	3.91 ± 0.81	st
3	109.83 ± 4.57	1.50 ± 0.20	m	108.31 ± 4.43	1.37 ± 0.16	m
4	102.83 ± 4.11	3.65 ± 0.41	st	101.92 ± 3.12	3.87 ± 0.52	st
5*	95.66 ± 5.50	3.74 ± 0.21	st	*94.32 ± 4.57	3.94 ± 0.15	st
6	90.83 ± 4.79	3.90 ± 0.45	st	89.71 ± 4.11	4.11 ± 0.29	st
7	63.16 ± 2.48	2.00 ± 0.24	sm	63.00 ± 3.97	1.98 ± 0.13	sm
8	55.00 ± 2.89	1.23 ± 0.24	m	54.98 ± 2.14	1.01 ± 0.32	m
9	51.16 ± 2.99	1.26 ± 0.20	m	52.83 ± 3.81	1.16 ± 0.72	m
10	47.83 ± 3.54	1.38 ± 0.09	m	47.93 ± 4.69	1.46 ± 0.12	m
11	42.66 ± 3.72	1.10 ± 0.10	m	41.36 ± 3.73	1.27 ± 0.33	m
12	37.50 ± 5.08	1.10 ± 0.12	m	37.00 ± 2.04	1.24 ± 0.12	m
13	29.16 ± 7.02	∞	t	28.16 ± 1.35	∞	t
14	22.66 ± 6.68	1.01 ± 0.04	m	21.94 ± 4.41	1.15 ± 0.31	m

Table 3.—Summary of the information available about the karyotypes of the species of *Eupsophus*.

Species	2N	NF	No. biarmed chromosomes	No. telocentric chromosomes	Source
E. emiliopugini	28	56	28	0	This paper
E. vertebralis	28	54	26	2	(Bogart 1970). This paper
E. roseus	30	46	16	14	(Iturra & Veloso 1989)
E. calcaratus	30	46	16	14	(Formas 1980)
E. migueli	30	45 male 46 female	15 male 14 female	15 male 16 female	(Iturra & Veloso 1989)

of *E. vertebralis* and *E. emiliopugini*. Both frogs have the same chromosomal formula (2N = 28), but the fundamental number is different (*E. emiliopugini* 56 and *E. vertebralis* 54), and the morphology of pair 13 is different (telocentric in *E. vertebralis* and metacentric in *E. emiliopugini*). The following hypothesis is offered to explain the evolution of karyological difference between *E. vertebralis* and *E. emiliopugini*: there was a pericentric inversion in the telocentric pair 13, which shifted the centromere to a metacentric position in *E. emiliopugini*. The similarity in size of pair 13 in both species supports the inversion mechanism. Though an inversion in chromosome pair 13 is a reasonable hypothesis there is at least one alternative possibility.

King (1980) explained the chromosome evolution of some frog species (*Litoria meiriana, L. chloris, L. phyllochroa, L. pearsoni,* and *L. olongburensis*) by addition of heterochromatin. In these events the relative chromosome arm lengths are modified to the same degree as the amount of C-banded chromatin added. The best example is seen in *Litoria meiriana* where a polymorphism for a large telomeric addition of a block of heterochromatin occurs on pair 12. On the basis of these observations an alternative hypothesis for the evolution of the karyological differences between *E. vertebralis* and *E. emiliopugini* would be that the addition of a heterochromatic segment in the centromeric region of the telocentric pair 13 led to the metacentric pair 13 of *E. emiliopugini*. C-band data could be used to test both hypotheses or perhaps, to suggest alternative ones. Chromosomal data has been useful to establish relationships among frogs. Chromosomal similarities among the five karyotypically known *Eupsophus* species (Table 3), allow recognition of two groups: the *vertebralis* group (2N = 28) (*E. vertebralis* and *E. emiliopugini*) and the *roseus* group (2N = 30) (*E. roseus, E. migueli* and *E. calcaratus*). Species of *vertebralis* group species have few telocentric chromosomes (0–2), whereas those of the *roseus* group are characterized by having many (14–16). Within the *roseus* group, Iturra & Veloso (1989) demonstrated the existence of sex chromosomes in *E. migueli* and *E. roseus*. The presence of sex chromosome dimorphism in both species, compared to the isomorphism founded in *E. calcaratus, E. vertebralis, E. emiliopugini* and other lower telmatobines frogs, is probably apomorphic.

Acknowledgments

I am grateful to Carlos Varela, Lila Brieva and Gonzalo Aguilar for field assistance, and Sonia Lacrampe for assistance in laboratory. I thank Dr. Milton Gallardo and two anonymous referees for their comments about the manuscript. This work was supported by Proyecto de Investigación S 89-6, Dirección de Investigación Universidad Austral de Chile and Proyecto 0050-89, Comisión Nacional de Investigación Científica y Tecnológica.

Literature Cited

Bogart, J. P. 1970. Systematic problems in the family Leptodactylidae (Anura) as indicated by karyological analysis.—Cytogenetics 9:369–383.

———. 1981. Chromosome studies in *Sminthillus* from Cuba and *Eleutherodactylus* from Cuba and Puerto Rico (Anura, Leptodactylidae).—Life Sciences Contributions Royal Ontario Museum 129:1–22.

Donoso-Barros, R. 1976. *Eupsophus vittatus* Philippi: revalidación de una buena especie.—Resúmenes Comunicaciones Sociedad de Biología de Chile 17:19.

Formas, J. R. 1980. The chromosome of *E. calcaratus* and the karyological evolution of the genus *Eupsophus* (Anura: Leptodactylidae).—Experientia 36:1163–1164.

———. 1989a. A new species of *Eupsophus* (Amphibia: Anura: Leptodactylidae) from southern Chile.—Proceedings of the Biological Society of Washington 102:568–576.

———. 1989b. Sinonimia e identidad de la rana austral chilena *Eupsophus vittatus* (Philippi, 1902) (Anura, Leptodactylidae).—Boletín Sociedad de Biología de Concepción, Chile 60:123–127.

Iturra, P., & A. Veloso. 1981. Evidence for heteromorphic sex chromosomes in male amphibians (Anura-Leptodactylidae).—Cytogenetics Cell Genetics 31:108–110.

———. 1989. Further evidence for early sex chromosome differentiation of Anuran species.—Genetica 78:25–31.

King, M. 1980. C-banding studies on Australian hylid frogs: secondary constriction structure and the concept of euchromatin transformation.—Chromosoma 80:191–217.

Levan, A., K. Fredga, & A. A. Sandberg. 1964. Nomenclature for centromeric positions on chromosomes.—Hereditas 52:201–220.

Menzies, J. I., & J. Tippet. 1976. Chromosome numbers of Papuan hylid frogs and karyotype of *Litoria infrafrenata* (Amphibia, Anura, Hylidae).—Journal of Herpetology 10:167–173.

Instituto de Zoología, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 12–22

THE GENUS *SCHIZODON* (TELEOSTEI: OSTARIOPHYSI: ANOSTOMIDAE) IN VENEZUELA, A REAPPRAISAL

Richard P. Vari and Sandra J. Raredon

Abstract.—*Schizodon fasciatus corti* Schultz (1944b) is shown to be a distinct species, *S. corti,* endemic to the Lago Maracaibo system. *Schizodon corti* can be distinguished from its congeners in northern South America by a combination of meristic and morphometric features and details of pigmentation. *Schizodon corti* is also characterized by distinctive sexually dimorphic modifications of the full pleural ribs in males. These modifications include a realignment of all ribs, the thickening of the first three full pleural ribs (on vertebrae 5, 6, 7), and an elongation and pronounced curvature of the first pleural rib. Initial citations of *Schizodon fasciatus* Agassiz and *S. isognathus* Kner from Venezuela by Günther (1864) and Peters (1877), respectively, are evaluated and are considered erroneous.

Resumen.—En este trabajo se demuestra que *S. fasciatus corti* Schultz (1944b) es realmente *S. corti,* una especie endémica del sistema del Lago de Maracaibo. *Schizodon corti* puede ser distinguida de sus congéneres distribuidos en el norte de America del Sur por una combinación de caracteres merísticas y morfométricos, así como detalles en la pigmentación. *Schizodon corti* se caracteriza también por poseer modificaciones sexuales dimórficas de las costillas pleurales de los machos. Estas modificaciones incluyen un rearreglo de todas las costillas, el engrosamento de las primeras tres costillas pleurales (sobre los vértebras 5, 6, 7) y el alargamiento y curvatura pronunciada de la primera costilla pleural. Citas iniciales de *S. fasciatus* Agassiz y *S. isognathus* Kner para Venezuela por Günther (1864) y Peters (1877), respectivamente, son evaluades y son considerades erroneas.

In his series of faunal studies of the fishes of Venezuela, Schultz (1944a, 1944b, 1949) described over 60 species and subspecies representing a diversity of freshwater and marine fish groups. One of these subspecies was *Schizodon fasciatus corti* Schultz (1944b:269), an anostomid characiform widespread in the rivers draining into Lago Maracaibo. Although the type-series for the subspecies was extensive, consisting of a holotype and 51 paratypes, Schultz incorporated data from only a subset of those specimens in the original description. The presented morphometrics for the subspecies were based on two specimens, the 257 mm holotype and an unspecified 222 mm SL paratype. Similarly the meristic data in Schultz's table 8 was drawn from an unspecified but obviously small subset of paratypes of varying composition.

In his key to the species of *Schizodon* reported from Venezuela, Schultz separated *S. fasciatus corti* from *S. fasciatus* Agassiz (in Spix & Agassiz 1829) and *S. isognathus* Kner (1859) based on details of pigmentation, differences in the numbers of scales in

the transverse series from the lateral line to the dorsal- and anal-fin origins, and in differences in the numbers of gill rakers. Schultz did not, however, expound on his decision to recognize that sample as a subspecies rather than a species. Neither did he discuss his alignment of his new subspecies with *fasciatus* rather than with *isognathus* or some other nominal species of *Schizodon*. We can only surmise that Schultz proposed that alignment based on the similarities in body form and coloration of the Lago Maracaibo *Schizodon* population and the two specimens of *S. fasciatus* which he used in his comparisons.

In the course of a study of the genus *Schizodon* in northern South America, we re-examined the majority of Schultz' specimens from Lago Maracaibo, one of the two specimens of *S. fasciatus* used in his comparisons, and other specimens of the genus from diverse regions of the continent. It became apparent that the Lago Maracaibo population was a species distinct from *S. fasciatus*. Indeed, the examination of the available series of *Schizodon* from Venezuela failed to confirm the presence of *S. fasciatus* in that country contrary to various literature citations. Those same studies also raised questions about the reported occurrence of *S. isognathus* in the Río Orinoco basin. In this paper we redescribe Schultz's form based on the portion of the type-series that remains at USNM and detail its distinguishing features. We also comment on the other species of *Schizodon* previously cited from Venezuela.

Materials and methods.—Counts and measurements were made following the methods outlined in Vari (1989), with the exception of lateral line scale counts which include all pored scales to the end of the series. Ranges for meristic and morphometric features include values of all examined specimens, unless otherwise noted. Values in square brackets are those of the holotype. Subunits of the head are presented as proportions of head length (HL). Head length itself and measurements of body parts are presented as proportions of standard length (SL). Transverse series from the lateral line to the origins of the anal and dorsal fins often include a much smaller scale at the bases of these fins which is herein reported as "½" scale following previous practice. Locality data and information on examined specimens are presented in the format detailed in Vari (1989).

The following abbreviations for institutions are used: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); British Museum (Natural History), London (BMNH); California Academy of Sciences, San Francisco (CAS); Stanford University, now deposited in CAS (CAS-SU); Indiana University, now deposited at CAS (IU); Museum of Comparative Zoology, Cambridge (MCZ); Muséum d'Histoire naturelle, Geneva (MHNG); Muséum national d'Histoire naturelle, Paris (MHNH); Museé d'Histoire naturelle de Neuchâtel (MHNN); Museo de Biologia, Universidad Central de Venezuela, Caracas (MBUCV); University of Michigan, Museum of Zoology, Ann Arbor (UMMZ); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and Instituut voor Taxonomische Zoölogie, Zoölogisch Museum, Amsterdam (ZMA).

Schizodon corti Schultz
Figs. 1–3

Piabuca schizodon Valenciennes, *in* Cuvier & Valenciennes 1849:112 [in part; syntype from Lago Maracaibo].—Bertin 1948:31 [listing of syntypes; syntype from Venezuela, Lago Maracaibo].—Fowler 1950:212 [in part, based on Cuvier & Valenciennes 1849; Lago Maracaibo citation].

Schizodon fasciatum corti Schultz 1944b: 269, figs. 30, 31a [type locality: Venezuela, Maracaibo Basin, Río Palmar near To-

tuma, about 100 km SW of Maracaibo].—Mago-Leccia 1970:76 [Venezuela].—Rodríquez 1973:288 [Lago Maracaibo; common name].

Diagnosis.—*Schizodon corti* can be distinguished from the other species of *Schizodon* that occur in northern South America on the basis of various meristic and morphometric features along with details of pigmentation. *Schizodon corti* has 5½ scales in a transverse series between the lateral line and the origin of the dorsal fin in contrast to 4½ scales in that series in *S. fasciatus* and the *Schizodon* species (hereafter termed *Schizodon* sp.) widespread in the Río Orinoco system (Géry et al. (1987:378–379), report 4 scales in that series in the holotype of *Schizodon fasciatus* (MHNN 781)). *Schizodon corti* has 5 scales between the lateral line and the origin of the anal fin contrary to 4 scales in that series in *S. fasciatus,* and 4 or 4½ in that series in *Schizodon* sp. The presence of three cusps on all jaw teeth in *Schizodon corti* readily discriminate that species from both *S. fasciatus* and *Schizodon* sp. which have 4 cusps. In *S. corti* the fourth blotch of dark pigmentation on the mid-lateral surface of the body is centered distinctly anterior of the vertical line through the origin of the adipose fin, whereas in *S. fasciatus* that pigmentation patch is located along that vertical line. *Schizodon corti* is further distinguished from *Schizodon* sp. in its relatively longer postorbital portion of the head (0.40–0.47 of HL versus 0.36–0.40), and in lacking the dark mid-lateral stripe found in *Schizodon* sp.

Description.—Body elongate, slightly compressed laterally in specimens under approximately 200 mm SL, nearly rotund in cross section in larger specimens. Dorsal profile of head distinctly convex from upper lip to vertical line through anterior nares, nearly straight from that line to posterior margin of head. Dorsal profile of body smoothly curved from rear of head to origin of dorsal fin, somewhat more convex in largest specimens; straight and posteroventrally slanted at base of dorsal fin, straight or gently convex from base of ultimate dorsal-fin ray to caudal peduncle. Dorsal surface of body with indistinct median keel anterior to dorsal fin, keel more obvious in specimens under 100 mm SL; body surface posterior to dorsal fin smoothly rounded transversely. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Pre-pelvic region slightly flattened transversely; post-pelvic portion of body transversely rounded.

Greatest body depth at origin of dorsal fin, depth 0.21–0.29 [0.23]; snout tip to origin of dorsal fin 0.41–0.46 [0.41]; snout tip to origin of anal fin 0.82–0.87 [0.82]; snout tip to origin of pelvic fin 0.45–0.49 [0.45]; origin of dorsal fin to hypural joint 0.57–0.62 [0.62]. Distal margin of dorsal fin rounded to nearly straight; anterior branched ray approximately three times length of ultimate ray. Pectoral-fin margin rounded distally; length of pectoral fin 0.15–0.18 [0.15], extends posteriorly nearly to vertical line through origin of dorsal fin in smaller individuals, distinctly shorter in specimens over 200 mm SL. Distal margin of pelvic fin founded; length of pelvic fin 0.17–0.20 [0.17], extends about two-fifths of distance to origin of anal fin. Caudal fin forked, lobes rounded. Adipose fin well developed. Distal margin of anal fin straight or very slightly emarginate, anteriormost branched rays two and two-thirds to slightly over three times length of ultimate ray. Caudal peduncle depth 0.10–0.11 [0.10].

Head distinctly pointed in lateral profile; head length 0.21–0.25 [0.21]; jaws equal, mouth terminal; snout length 0.28–0.38 [0.33]; nares of each side separated by distance approximately equal to width of opening of posterior nares; anterior nares tubular, opening of posterior nares longitudinally ovoid; orbital diameter 0.22–0.29 [0.26]; length of postorbital portion of head 0.40–0.47 [0.43]; gape width 0.18–0.23 [0.22]; interorbital width 0.44–0.53 [0.50].

Pored lateral-line scales from supracleithrum to end of lateral line 43 to 45 [44]; all scales of lateral line pored; 5½ [5½] scales in transverse series from origin of dorsal fin to lateral line; 5 [5] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,10 [ii,10]; anal-fin rays ii,8 [ii,8]; pectoral-fin rays i,15–16 [i,15]; pelvic-fin rays i,8 [i,8].

Total vertebrae 40 (11), 41 (12) [40].

Dentition.—Teeth in upper jaw limited to premaxillae, 4 on each side. Teeth irregularly tricuspidate with two medial cusps distinctly larger, and lateral cusp relatively small. Four teeth on each side of lower jaw; form of dentary teeth similar to those in upper jaw (see also Schultz 1944b:fig. 31a for sketch of tooth form in the species).

Color in alcohol.—Most specimens in type-series retain some guanine on scales, somewhat silvery to golden, darker dorsally. Head dark dorsally, light yellow ventrally, without any notable pigmentation pattern. Body distinctly darker dorsally, with four patches of dark pigmentation along lateral surface. Patches ranging in form from uniformly dark, posteroventrally slanted bars to rotund dark spots centered ventral of lateral line. These spots are continuous dorsally with bar of less intense dark pigmentation (Figs. 1–3). Anterior margin of anteriormost dark body patch located along lateral line about three scales posterior of supracleithrum. Second patch of dark pigmentation located under base of dorsal fin. Third pigmentation patch on body located along vertical line midway between origin of dorsal and adipose fins. Fourth patch situated slightly anterior of vertical line through origin of anal fin. Dark rotund spot situated medial to terminal scales of lateral line and on base of middle rays of caudal fin. Pigmentation pattern of dark bars or rotund patches on body somewhat obscured in largest specimens examined. Holotype (Figs. 1–2) at extreme of range of variation in form of pigmentation patches, with patches of dark pigmentation much smaller than in most paratypes. Dark body patches in holotype continuous dorsally with less intensely pigmented bars. Most paratypes have posteroventrally slanted, uniformly dark bars along side of body (Fig. 3).

Dorsal, caudal and anal fins dusky. Adipose fin dusky basally, with distal half typically much darker. Pectoral and pelvic fins hyaline.

Distribution.—Rivers draining into Lago Maracaibo, Venezuela.

Common name.—According to Schultz (1944b:271) the common name of the species is "corti." Mago-Leccia (1970:76) and Rodríquez (1973:288), however, cite it as "cotí."

Sexual dimorphism.—Radiographs of the type-series of *Schizodon corti* revealed unusual sexual dimorphism in the morphology and position of the anterior pleural ribs. Females of the species have the anterior pleural ribs aligned roughly parallel to each other, with the individual ribs slanting only slightly posteroventrally. The anteriormost full pleural rib of each side in females is slightly thicker than the second, with the second through terminal pleural ribs progressively thinner. Males of *S. corti* have the first complete pleural rib of each side, on the fifth vertebrae, much more highly developed than in females of comparable sizes. The shaft of the bone is proportionally much thicker than in females, and the rib is both notably lengthened and has a more pronounced curvature of its distal portion than in females. In males over 200 mm SL this results in a thick, scimitar-shaped anteriormost pleural rib on each side, the tip of which extends posteriorly to the vertical line through the 13th to 15th vertebrae. The second and third full pleural ribs on each side in males (on vertebrae 6 and 7) are also relatively thicker and distinctly more posteroventrally slanted than in females, but differ from the first rib in not being recurved. The remaining pleural ribs in males of *S. corti* are straight and not thickened relative to comparable elements in females,

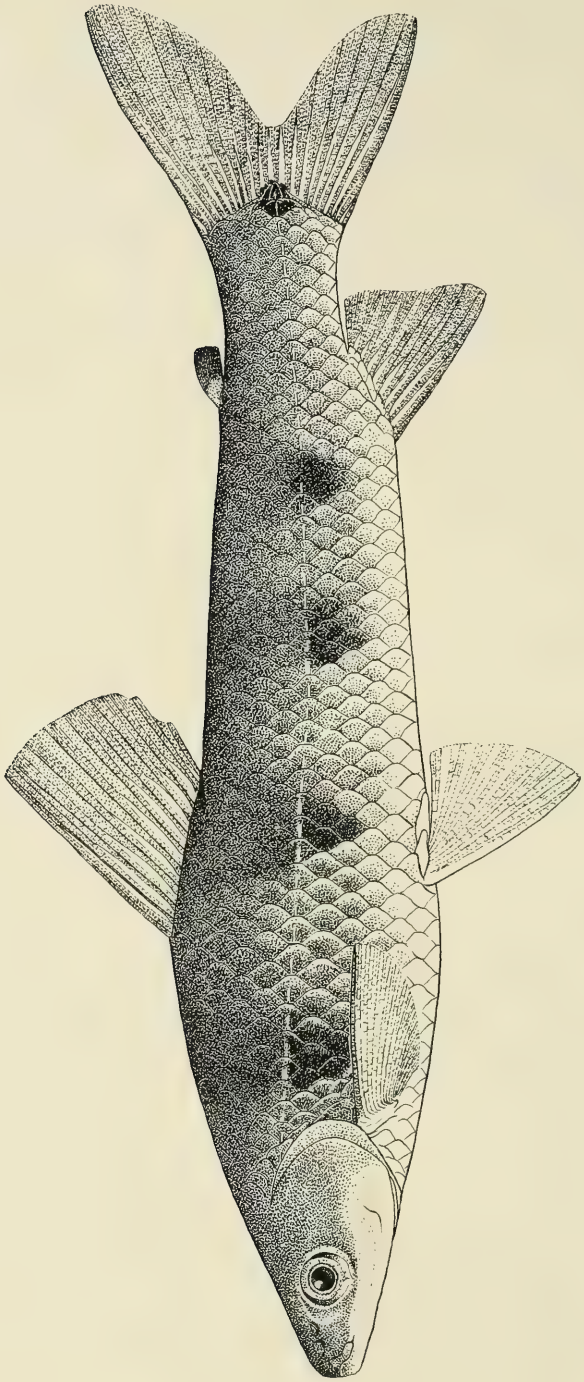


Fig. 1. *Schizodon corti,* USNM 121300, 257 mm SL; holotype of *Schizodon fasciatus corti*; Venezuela, Maracaibo basin, Río Palmar near Totuma, about 100 km SW of Maracaibo. Reproduction of original figure from Schultz (1944b:fig. 30).

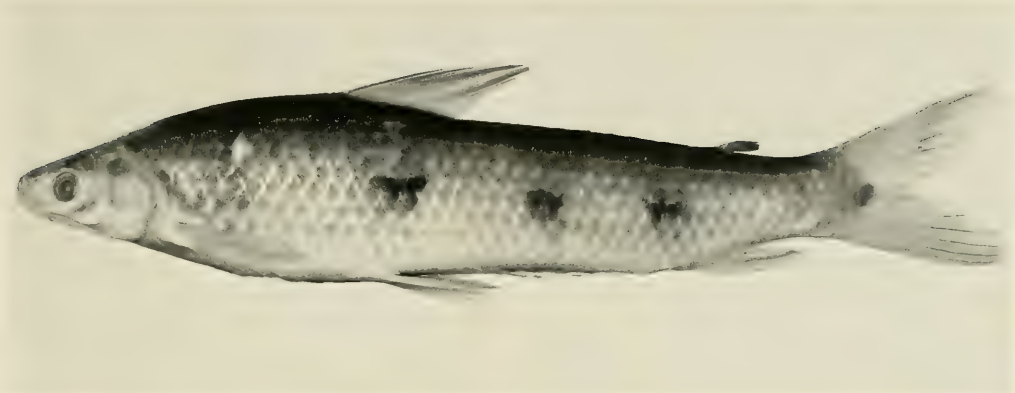


Fig. 2. *Schizodon corti,* USNM 121300, 257 mm SL; holotype of *Schizodon fasciatus corti*; Venezuela, Maracaibo basin, Río Palmar near Totuma, about 100 km SW of Maracaibo.

but are still notably more posteroventrally aligned than in females.

A less pronounced form of sexual dimorphism of the pleural ribs has been found in some individuals of *Schizodon fasciatus* in which the anteriormost full pleural rib on each side is somewhat thickened, but not lengthened as in *S. corti.* No indication of comparable modifications have been discovered in the radiographed specimens of *Schizodon* sp., most of which, however, are not as large as the type-series of *S. corti.* More extensive surveys of all nominal species of *Schizodon* are necessary to determine whether these pronounced modifications of the anterior pleural ribs in *S. corti* are autapomorphic for that species or also occur in other members of the genus.

Remarks.—We recognize the Lago Maracaibo *Schizodon* populations as a distinct species, *S. corti,* rather than as a subspecies of *S. fasciatus* given the differences between the two forms noted in the "Diagnosis" above. Interestingly the description of *Schizodon fasciatus corti* was predated by the description of another *Schizodon* species based, in part, on a specimen from the Maracaibo basin. Valenciennes *in* Cuvier & Valenciennes (1849), was the first researcher to report a specimen of what is now

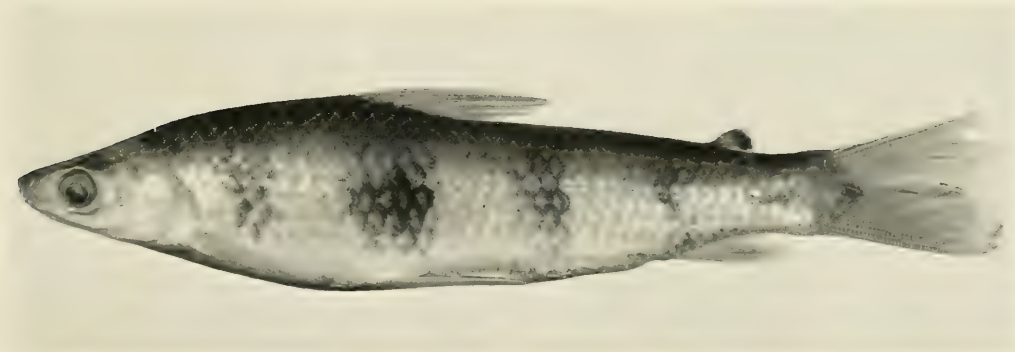


Fig. 3. *Schizodon corti,* USNM 121302, 188 mm SL; paratype of *Schizodon fasciatus corti*; Venezuela, Maracaibo basin, Río Palmar at bridge, 70 km SW of Maracaibo.

termed *Schizodon* from Lago Maracaibo. His description of *Piabuca schizodon* was based on a series of syntypes from Lago Maracaibo, the Amazon basin, and the Essequibo River of Guyana. *Piabuca schizodon* was first considered a synonym of *Schizodon fasciatus* by Eigenmann & Eigenmann (1891:50) followed by various authors (e.g., Fowler 1950). That decision was evidently based solely on literature information, without an examination of the syntype series. As noted, only one species of *Schizodon, S. corti,* is known from the Lago Maracaibo system and is endemic to that basin. The syntype series of *Piabuca schizodon* containing both one individual from Lago Maracaibo, and specimens from other portions of South America, is thus undoubtedly complex, presumably consisting of *Schizodon corti* and one or more of its congeners from the Rio Amazonas and Essequibo River.

In his description of *Schizodon fasciatus corti* Schultz (1944b:269) cited Valenciennes' description of *Piabuca schizodon* and noted its reported occurrence in Lago Maracaibo. Schultz did not, however, discuss the rationale behind his decision to describe a new subspecies rather than resurrecting *Piabuca schizodon* by designating the syntype of *Piabuca schizodon* that originated in the Lago Maracaibo basin as the lectotype of the species. Our decision to use the name proposed by Schultz, rather than the earlier name of Valenciennes is a consequence of information on the condition of the syntypes of the species published by Bertin (1948:31) subsequent to Schultz's paper (1944b). Bertin reported that the syntype of *Piabuca schizodon* from Lago Maracaibo (MNHN A.8643) was dry and in poor condition, whereas the alcohol preserved syntypes of the species from the Essequibo River (MNHN A.9840) and Rio Amazonas (MNHN A.9839) were in good condition. Thus the Lago Maracaibo specimen would be an unsuitable lectotype of *S. corti.* We could preemptively make the Valenciennes name unavailable for the Lago Maracaibo populations by designating one of the syntypes that originated in the Rio Amazonas or Essequibo River as the lectotype. We prefer not to follow that course of action given the uncertainty that exists concerning the species of *Schizodon* across much of South America, and in the absence of a reasonable knowledge of the geographic distributions of these forms. Rather, we leave that action to other colleagues who are in the process of completing a revisionary study of the Amazonian species in the genus.

Comments on other Schizodon species cited from Venezuela.—Two other species of *Schizodon* reported for Venezuela were included by Schultz (1944b:268) in his key to the species of the genus that occur in that country. *Schizodon fasciatus* was first reported as a component of the Venezuelan freshwater ichthyofauna by Günther (1864: 304). Subsequent citations of the species in Venezuela by Eigenmann & Eigenmann (1891:50), Eigenmann (1910:425), Eigenmann & Allen (1942:303), Fowler (1945: 125), Géry (1964:35), and Mago-Leccia (1967a:254, 1970:76) appear to have been based on the original Günther citation rather than additional specimens. Examination of the specimen cited by Günther (BMNH 1854.3.21:4) reveals that it is apparently *Schizodon fasciatus*; differing from *S. corti* in the various features noted in the "Diagnosis." The locality record cannot be confirmed on the basis of more recently collected specimens, and appears erroneous given the known distribution of *Schizodon fasciatus.* Günther (1864:304) cited the specimen as having come from "Caraccas," a locality interpreted by later workers as referring to Caracas, Venezuela. Eigenmann (1920, 1922) did not report *Schizodon fasciatus* for the collections from the Río Tuy basin that he examined. That isolated coastal drainage system of northern Venezuela includes the Río Guaire system, the river of the Valle de Caracas. Mago-Leccia (1967: 250), in his discussion of the fishes of the

Río Guaire, listed Günther's record of *Schizodon fasciatus* from Caracas as doubtful on the basis of the collections that he made in that river system. An examination of series of *Schizodon* from both the Venezuelan and Colombian portions of the Río Orinoco basin failed to reveal *S. fasciatus.* A check of the holdings of a number of museums, furthermore similarly failed to reveal any specimens of *Schizodon* from the Río Negro basin in the amazonian portions of Venezuela, and Goulding et al. (1988: 100–101) comment that *Schizodon* was not represented in the massive collections they examined from throughout the Brazilian portions of the Rio Negro basin.

Schultz did not specify which specimens served as the basis for the data on *S. fasciatus* used in his key to Venezuelan *Schizodon* (1944b:268) and in table 8 of that publication. An examination of the USNM holdings of *Schizodon* did not reveal any material from Venezuela which agrees with the information in that key and table. One USNM specimen identified as *S. fasciatus* (USNM 94626) has in the jar a slip of paper with notations in Schultz' handwriting on various meristic features of the specimen. Those data agree with the information for *S. fasciatus* in Schultz' key, and this specimen is apparently one of the two from which Schultz took data for *S. fasciatus.* This specimen originated, however, not in Venezuela, but rather in the headwaters of the Rio Juruá basin, a southern tributary of the Rio Amazonas, over 2200 river kilometers distant from the nearest border of Venezuela. It would appear that Schultz did not examine any Venezuelan *Schizodon fasciatus* in his study. In summary, we are unable to confirm the presence of *S. fasciatus* in Venezuela.

We are nonetheless left with the puzzling Günther citation (1864:304) of *S. fasciatus* from "Caraccas." Various explanations could account for that record. The locality may refer to a locality other than Caracas, Venezuela, or the specimen was perhaps collected at some distant locality and transhipped to Günther through Caracas. Finally it is possible that the reported data was erroneously associated with the specimen. The latter seems likely given that the number for the specimen (BMNH 1854.3.21:4) actually is assigned to a squirrel from Ceylon (=Sri Lanka) in the registers of the Department of Zoology, British Museum (Natural History) (G. J. Howes, in litt.).

A third nominal species, *Schizodon isognathus* Kner has been cited in the Río Orinoco system and included by Schultz (1944b: 268, 271) in his key to the Venezuelan members of the genus. Schultz presumably included *S. isognathus* in his key based on the report of that species in Venezuela by Peters (1877:472). Peters did not discuss the specimens he examined, only citing *Anostomus* (=*Schizodon*) *isognathus* from San Fernando de Apure in the central portions of the Río Orinoco basin. The only species of *Schizodon* that we have been able to locate among the series of *Schizodon* specimens from that region is the form termed *Schizodon* sp. in the "Diagnosis" (see also discussion below). *Schizodon isognathus,* originally described from the Río de La Plata basin, differs from *Schizodon* sp. in mouth position, in possessing dark vertical blotches on the body in small and moderate sized specimens, and in various meristic features. Schultz (1944b) did not detail the source of his information on *S. isognathus,* and we have been unable to locate any specimens in the USNM collections which would have been available to him and which agree with his data. The meristics for the species in his key agree exactly with the data in the original description of the species (Kner 1859), and the description of the pigmentation was evidently derived from that publication. In summary there is no evidence that *S. isognathus* actually occurs in the Río Orinoco system, and we assume that the Peter's record is a misidentification.

It is impossible at this time to be certain

of the identity of the specimens examined by Peters (1877). Two likely candidates can be identified, the first being *Schizodon* sp. Small through moderate sized specimens of that species have both diffuse dark vertical blotches and a dark mid-lateral, but in some of the largest specimens of the species the vertical blotches are faint or absent. Peters may have equated a large individual of *Schizodon* sp. with *Anostomus* (=*Schizodon*) *isognathus* which has a distinct mid-lateral stripe (see Géry et al. 1987:fig. 12). It is also possible that Peters' material was *Anostomus orinocensis* described by Steindachner (1879) from the Río Orinoco system and assigned to *Laemolyta* Cope (1872) by Myers (1950:197) and Géry (1977:182). *Laemolyta orinocensis* has an elongate body and a mid-lateral dark stripe on the body comparable to that of *Schizodon isognathus* (see Steindachner 1879:pl. II, fig. 7), but the two species differ in various meristic features, most notably the number of scales in the transverse series above and below the lateral line, and in the form of the teeth on the lower jaw.

Although no evidence has been found to support earlier citations of *Schizodon fasciatus* or *S. isognathus* in Venezuela, *S. corti* is not the only species of the genus occurring in that country. Another species, identified as *Schizodon* sp. in the "Diagnosis" above is widespread in the Río Orinoco basin. That species has a pattern of dark vertical blotches and a dark mid-lateral stripe, or only a mid-lateral stripe in larger individuals. As noted in the "Diagnosis" it differs from *S. corti* in its pigmentation patterns and various aspects of meristics and dentition. It appears that the species is undescribed, but we prefer to place that question into abeyance until more information is available on the recognizable species of *Schizodon* in the river systems adjoining the Orinoco basin.

Material examined.—*Schizodon corti*: (all collected in Venezuela, Maracaibo basin), Río Palmar near Totuma, about 100 km SW of Maracaibo; USNM 121300 1 (257.0, holotype of *S. fasciatus corti*); (all remaining specimens are paratypes of *S. fasciatus corti*), Río Palmar near Totuma, about 100 km SW of Maracaibo; USNM 121306, 10 (166.0–334.0). Caño ½ km W of Sinamaica, USNM 121301, 3 (152.7–177.0; originally 4 specimens in lot, 1 specimen exchanged to J. Géry and subsequently transferred to MHNG). Río Palmar at bridge, 70 km SW of Maracaibo; USNM 121302, 3 (188.0–230.0 mm; originally 4 specimens cited in lot, 1 specimen exchanged to ZMA). Río Motatán at the bridge, 22 km N of Motatán; USNM 121303, 1 (approximately 285). Río Negro below mouth of Río Yasa; USNM 121304, 2 (approximately 280 and 290 mm). Río Apon about 35 km S of Rosario; USNM 121305, 5 (235.0–265.0). Río Socuy, 3 km above its mouth; USNM 121307, 8 (129.6–309.0, originally 15 specimens cited in lot, 5 specimens exchanged to UMMZ, 2 specimens exchanged to MCZ).

Schizodon fasciatus: "Caraccas," BMNH 1854.3.21:4, 1 (161.3). BRAZIL. Amazonas. Rio Madeira, CAS-SU 22065, 1 (215.0). Paraná de Lago Janauacá, entrance to Lago do Castanho, USNM 229056, 2 (84.1–134.2). Mouth of Rio Embira, near Envira, tributary of Rio Tarauacá, Rio Juruá system (7°30′S, 70°15′W), USNM 94626, 1; AMNH 12546, 1 (202.0). PERU. Río Ucayali basin, Boca Chica, ANSP 73181, 6 (1, 171.3). Loreto. Río Pachitea, Iparia Reserve, 1 km SE of Tournavista, ANSP 119893, 1 (161.2). Río Ampiyacu, near Pebas, CAS-SU 36939, 2 (123.8–146.2). Iquitos fish market, USNM 280716, 1. BOLIVIA. Beni. Río Itenez, 1 km downstream (W) of Costa Marquez, Brazil, AMNH 40098, 4 (201–210). Riberalta, near Río Beni, ANSP 120355, 1 (250). Río Baures, 2 km above mouth, Río Itenez system, UMMZ 204875, 6. GUYANA. Rupununi. Rupununi River, ANSP 39737, 1. Twoca Pan, CAS 15784, 1 (formerly IU 12417).

Schizodon sp.: VENEZUELA. Apure. Río Cunaviche, at Cunaviche, USNM 258268, 10 (6, 91.0–112.3). San Fernando de Apure,

esteros on S bank of Río Apure, approx. 3 km W of Fisheries Station, USNM 258267, 11. Merecure (Los Guanotas) near San Fernando de Apure, USNM 307950, 3. Side Channel of Río Apure, approx. 3 km W of center of San Fernando de Apure, USNM 258017, 2. Monagas. Isla Chivera, Caño Chivera, near Barrancas (8°41′N, 62°10′W), USNM 233857, 3. Barinas. Río Nitiado-Seco, USNM 194214, 4. Río Las Palmas, USNM 311074, 3. Portuguesa. Río Maria at bridge on Guanare to Acarigua highway, CAS 64327, 3.

Acknowledgments

Dr. Antonio Machado-Allison and Dr. Francisco Mago-Leccia generously provided work space at MBUCV and provided access to the holdings of *Schizodon* in their care. Dr. Carl Ferraris and Ms. Barbara Brown (AMNH), Mr. William G. Saul (ANSP); Mr. Gordon J. Howes (BMNH), Mr. David Catania (CAS), Mr. Karsten Hartel (MCZ), and Mr. Douglas Nelson (UMMZ) assisted us with loans and information concerning *Schizodon* specimens in their collections. Dr. Antonio Machado-Allison (MBUCV) generously provided the Spanish translation of the Abstract. Mr. Jeffrey Clayton (USNM) prepared Fig. 1. Figures 2 and 3 were prepared by Mr. Theophilus Britt Griswold. This paper benefitted from the comments and suggestions of Dr. Thomas A. Munroe (National Marine Fisheries Service, Systematics Laboratory), Dr. Stanley H. Weitzman (USNM), Dr. Wayne C. Starnes (USNM), and Dr. Scott A. Schaefer (ANSP). Research associated with this project in Venezuela and Brazil was supported by the I.E.S.P. Neotropical Lowland Research Program of the Smithsonian Institution.

Literature Cited

Bertin, L. 1948. Catalogue des types de poissons du Muséum national d'Histoire naturelle. 3e partie. Ostariophysaires (Characiniformes, Gymnotiformes).—Bulletin du Museum national d'Histoire Naturelle, Paris 3:1–51.

Cope, E. D. 1872. On the fishes of the Ambiyacu River.—Proceedings of the Academy of Natural Sciences of Philadelphia 23:250–294.

Cuvier, G., & A. Valenciennes. 1849. Histoire Naturelle des Poissons, volume 22, Paris, 395 pp.

Eigenmann, C. H. 1910. Catalogue of the freshwater fishes of tropical and south temperate America.—Report of the Princeton University Expedition to Patagonia, 1896–1899 3(4):375–511.

———. 1920. The fishes of Lake Valencia, Caracas and the Rio Tuy at El Concejo, Venezuela.—Indiana University Studies 7(44):1–13.

———. 1922. The fishes of western South America, Part 1. The fresh-water fishes of northwestern South America, including Colombia, Panama, and the Pacific slopes of Ecuador and Peru, together with an appendix upon the fishes of the Rio Meta in Colombia.—Memoirs of the Carnegie Museum 2:1–346.

———, & W. R. Allen. 1942. Fishes of western South America. I. The intercordilleran and amazonian lowlands of Peru. II. The high pampas, Bolivia, and northern Chile; with a revision of the Peruvian Gymnotidae, and of the genus *Orestias*. University of Kentucky, Lexington, 494 pp.

———, & R. S. Eigenmann. 1891. A catalogue of the fresh-water fishes of South America.—Proceedings of the United States National Museum 14: 1–81.

Fowler, H. W. 1945. Los peces del Perú.—Boletín Museo de Historia Natural "Javier Prado," Lima 7:1–298.

———. 1950. Os peixes de água doce do Brasil (2a entrega).—Arquivos de Zoologia do Estado de São Paulo 6:205–401.

Géry, J. 1964. Poissons characoïdes de l'Amazonie péruvienne.—Beiträge zur Neotropischen Fauna 4(1):1–44.

———. 1977. Characoids of the world. TFH Publications, Neptune City, New Jersey, 672 pp.

———, V. Mahnert, & C. Dlouhy. 1987. Poissons characoïdes non Characidae du Paraguay (Pisces, Ostariophysi).—Revue Suisse de Zoologie 94(2):357–464.

Goulding, M., M. Leal Carvalho, & E. G. Ferreira. 1988. Rio Negro, rich life in poor water. Amazonian diversity and foodchain ecology as seen through fish communities. The Hague, SPB Academic Publishing, 200 pp.

Günther, A. 1864. Catalogue of the fishes in the collection of the British Museum, volume 5. London, 455 pp.

Kner, R. 1859. Zur familie der Characinen. III. Folge der ichthyologischen beiträge.—Denkschriften der Akademie der Wissenschaften, Wien 17:137–182.

Mago-Leccia, F. 1967a. Notas preliminares sobre los peces de los Llanos de Venezuela.—Boletin de la Sociedad Venezolana de Ciencias Naturales, Caracas 17(112):237–263.

———. 1967b. Notas sobre los peces del Río Guaire.—Estudio de Caracas, Universidad de Venezuela, Caracas 1:227–256.

———. 1970. Lista de los peces de Venezuela. Ministerio de Agricultura y Cria, Caracas, 241 pp.

Myers, G. S. 1950. Studies on South America freshwater fishes II. The genera of Anostomine characids.—Stanford Ichthyological Bulletin 3(4): 184–198.

Peters, W. 1877. Über die von Hrn. Dr. C. Sacks in Venezuela gesammelten Fische.—Monatsbericht der Akademie der Wissenschaften zu Berlin 469–473.

Rodríquez, G. 1973. El sistema de Maracaibo. Biología y Ambiente. Instituto Venezolano de Investigaciones Cientificas, Caracas, 395 pp.

Schultz, L. P. 1944a. The catfishes of Venezuela, with descriptions of thirty-eight new forms.—Proceedings of the United States National Museum 94(3172):173–338.

———. 1944b. The fishes of the family Characinidae from Venezuela, with descriptions of seventeen new forms.—Proceedings of the United States National Museum 95(3181):235–367.

———. 1949. A further contribution to the ichthyology of Venezuela.—Proceedings of the United States National Museum 99(3225):1–211.

Spix, J. B. von, & L. Agassiz. 1829. Selecta genera et species piscium quos in itinere per Braziliam annis 1817–20 perecato collegit J. B. de Spix. Munich, 138 pp.

Steindachner, F. 1879. Beiträge zur kenntniss der flussfische Südamerika's.—Denkschriften der Akademie der Wissenschaften, Wien 41:151–172.

Vari, R. P. 1989. Systematics of the neotropical characiform genus *Curimata* Bosc (Pisces: Characiformes).—Smithsonian Contributions to Zoology 474:1–63.

Department of Vertebrate Zoology (Fishes), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 23–29

PLATYCEPHALUS CHAULIODOUS, A NEW FLATHEAD FISH FROM THE EASTERN INDIAN OCEAN (TELEOSTEI: PLATYCEPHALIDAE)

Leslie W. Knapp

Abstract.—A new platycephalid, *Platycephalus chauliodous,* is described from seven specimens collected near Perth, Western Australia. This species is distinguished from other members of *Platycephalus* Bloch, 1795 and from *Neoplatycephalus* Castelnau, 1872 by its distinctive color pattern, by the unusual combination of fourteen dorsal and thirteen anal-fin rays, by the large canines on tooth-bearing bones and by the low number (59–65) of pored lateral line scales.

In 1973, a large specimen (453 mm SL) of an undescribed species of Platycephalidae was speared near Carnac Island, Western Australia. The specimen was frozen and transported to the Western Australian Museum where Dr. J. Barry Hutchins, recognizing the specimen as being distinctive, sent it to the author. Since 1973, six additional specimens have been found, all coming from Western Australian localities near Perth. The new species is described here and compared to congeners, as well as to the species currently assigned to *Neoplatycephalus* Castelnau, 1872. *Neoplatycephalus* has been variously recognized as a genus (Waite 1921, Hutchins & Swainston 1985) or as a subgenus of *Platycephalus* (McCulloch 1927, Knapp 1987). Recent electrophoretic and morphological studies of the relationships within the family Platycephalidae indicate that *Neoplatycephalus* merits generic recognition (C. P. Keenan, pers. comm.).

The new species shares the specialized feature of vomerine teeth in a single, crescent-shaped patch with species of *Platycephalus* and *Neoplatycephalus.* It shares the presence of large canine teeth with *Neoplatycephalus.* According to May (1986), the three species currently placed in *Neoplatycephalus* are taken in temperate waters of southern Australia at the following depths: *N. aurimaculatus,* 80–100 m; *N. conatus,* 70–420 m; and *N. richardsoni,* 10–170 m, sometimes entering coastal bays. Depth records for the new species indicate that it is taken from 0–40 m, usually 10 m or less. On the basis of the large canine teeth and the close proximity of its geographic range to that of *Neoplatycephalus,* one might regard the new species as a shallow water representative of *Neoplatycephalus.* However, comparison of the new species with those of *Neoplatycephalus* (Table 1) indicates that major differences exist.

The new species has a lower number of lateral line scales (59–65), a combination of 14(15) dorsal-fin rays and 13(14) anal-fin rays, interorbital space larger than orbit diameter (adults), preocular spine lacking, preopercular spines about equal in length, suborbital bone more narrowly bicarinate, usually 11 branched caudal-fin rays, and the rear edge of the maxilla is below or in front of the anterior margin of the orbit. Also, the diameter of the round eye of the new species is small, going 1½ to 2 times into the diameter of the oval-shaped eye found in the species of *Neoplatycephalus.* Finally, the large canine teeth on the dentary of the new species become smaller anteriorly and are lacking from the anteriormost quarter of the jaw. Canines on the lower jaw of *Neoplaty-*

Table 1.—Comparison of characters between *Platycephalus chauliodous* and species of *Neoplatycephalus*. Mean or usual condition given in parentheses.

Character	*P. chauliodous*	*N. aurimaculata*	*N. conatus*	*N. richardsoni*
Pored lateral-line scales	59–65 (63)	81–85	72–78	64–74 (69)
Anal-fin rays	13–14 (13)	13–14 (14)	13–14 (14)	14
Gill rakers	2+9–10 (9)	1+5–7	1–2+7–10	3+10–12
Large teeth at front of dentary	absent	present	present	present
Interorbital width (adults)	larger than eye	smaller	smaller	smaller
Length of preopercular spines	about equal	lower longest	lower longest	lower longest
Branched caudal-fin rays	usually 11	usually 12	12–13	12–13
Suborbital bone bicarinate	narrowly	broadly	broadly	broadly
Rear edge of maxilla	to front of eye	past front of eye	past front of eye	past front of eye
Top of head	naked	scaly	scaly	scaly
Umbraculum	broadly lobate	simple lobe	simple lobe	simple lobe

cephalus species are more or less evenly spaced along the entire length of the jaw.

The differences between the new species and the three species of *Neoplatycephalus* are significant. Additionally, *N. aurimaculatus, N. conatus,* and *N. richardsoni* appear to form a natural group. Therefore, the new species is here provisionally placed in *Platycephalus.*

Methods.—Counts and measurements follow those of Knapp (1973), except that standard (SL), head and snout lengths listed here, were measured from the tip of the snout. Type material is deposited at the following institutions: American Museum of Natural History (AMNH); Australian Museum, Sydney (AMS); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and the Western Australian Museum, Perth (WAM). Other institutions listed are: Academy of Natural Sciences, Philadelphia (ANSP); California Academy of Sciences (CAS-SU); Commonwealth Science and Industrial Research Organization, Hobart, Tasmania (CSIRO); National Museum of Victoria, Melbourne (NMV); Naturhistorisches Museum, Wien 1, Austria (NMW); Northern Territory Museum of Arts and Sciences, Darwin (NTM); Staatliches Museum for Naturkunde in Stuttgart (SMNS); and Universitat Humboldt, Berlin (ZMB). Material of other species used for comparative purposes in text and tables appears in Appendix 1.

Platycephalus chauliodous, new species
Figs. 1–3, Tables 1–3

Platycephalus sp. Hutchins & Thompson, 1983:28, 78, fig. 115.

Neoplatycephalus sp. Hutchins & Swainston, 1985:46, 127, fig. 196.

Material examined.—Holotype, AMS I.20231-007 (304 mm SL), Western Australia, Cockburn Sound, ½ km S Carnac Island, 6–7 m, Barry C. Russell, 27 Mar 1978.

Six paratypes: Western Australia: WAM P24172-001 (453), Cockburn Sound, Carnac Island, 3 mi off Freemantle, ca. 10 m, B. Paxman, 30 Dec 1973. WAM P25798-008 (66), Eagle Bay, 33°33.5′S, 115°04′E, 0–4 m, Gerald R. Allen and party, 21 Oct 1976. WAM P29879.001 (332), 31°50′S, 115°44′E, ca. 40 m, Ian Beaumont, Dec 1988. WAM P29944.001 (399), Cowaramup Beach, 33°47′S, 115°00′E, ca. 8 m, D. Axcell, 19 Feb 1989. USNM 307398 (77), off Garden Island, 32°12′S, 115°40′E, G. R. Allen, 10 Apr 1976. AMNH 48856 (216), Cape Freycinet, 0–6 m, Donn E. Rosen and party, 22 Mar 19. Material of other species

used for comparative purposes in text and tables appears in Appendix 1. As Matsubara & Ochiai (1955) and Hughes (1981) have pointed out, the configuration of pored lateral line scales in Platycephalidae can be unique to a species or similar in several closely related species. Descriptions of new species of flatheads should include illustrations of the pored scales whenever possible.

Diagnosis. —A species tentatively assigned to the genus *Platycephalus* Bloch, with 14(15) dorsal-fin rays and 13(14) anal-fin rays, a low number (59–65) of pored lateral line scales, and large canines on tooth-bearing bones in the mouth.

Description. —Values for holotype in parentheses. Dorsal-fin rays 0–I,VII,I,14–15(14); anal-fin rays 13–14(13); pectoral-fin rays 19–20(19), usually 1+13+5; pelvic-fin rays I,5; pored lateral line scales 59–65(64), lacking spines; scales above lateral line slanting downward and backward 90–100(100); diagonal scales 14–18(14); interpelvic scales 31–35(31); gill rakers 2+9–10(2+9); branched caudal-fin rays 10–11(11). Measurements for the holotype and paratypes appear in Table 2. Least interorbital width greater than diameter of eye in specimens 216 mm SL and larger, only about ½ eye diameter in specimens 77 mm SL and smaller; first dorsal spine triangular, about as long as spine base is wide, length 16–24(16) times into second spine in specimens 216 mm SL and greater. Nape covered with scales, top of head naked, a few embedded scales on opercle and cheek. Preocular spine lacking. Infraorbital ridge low, ending in a fan-shaped series of 3–4 short ridges; several other low ridges on head behind infraorbital ridge. Suborbital ridge smooth. Two preopercular spines present of about equal length. Intraopercular flap absent, membrane with scalloped edge. Lower opercular spine short, upper opercular spine concealed under skin. Rear edge of maxilla in front of or just below anterior margin of orbit. Upper jaw with several rows of small

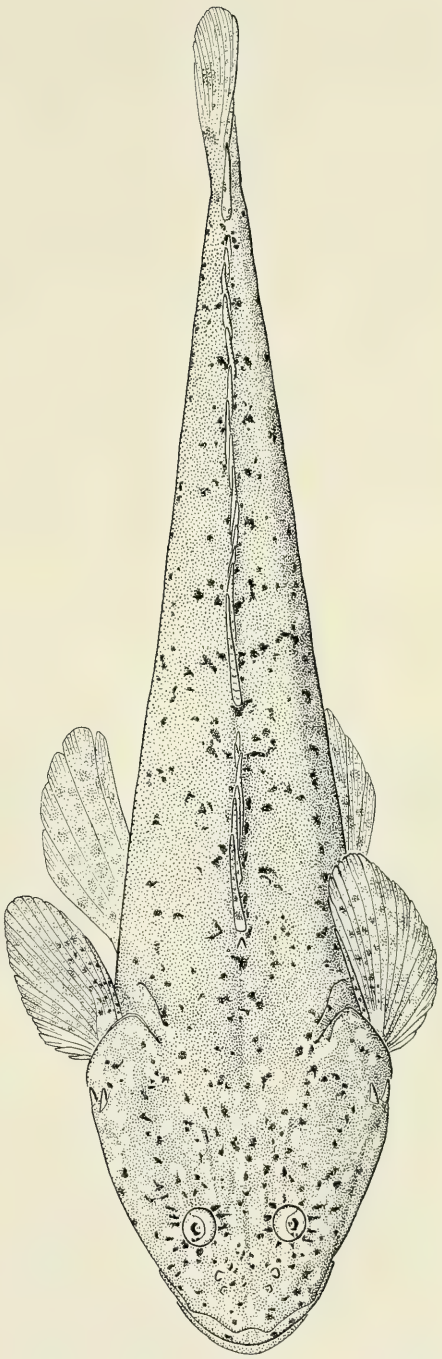


Fig. 1. *Platycephalus chauliodous*, new species, AMS I.20231-007, holotype, 304 mm SL, dorsal view, from off Carnac I., Western Australia.

Table 2.—Proportional measurements of *Platycephalus chauliodous* expressed in thousandths of standard length.

Character	Holotype	Paratypes	
		Range	Mean
Standard length (mm)	304.0	66.0–453.0	257.2
Head length	319.1	300.0–333.3	316.2
Snout length	92.4	88.5–110.4	101.0
Orbit diameter (greatest)	34.2	31.6–68.2	43.8
Interorbital width (least)	47.0	31.8–50.4	43.7
First dorsal spine length	5.9	4.6–36.4	15.1
Second dorsal spine length	95.4	88.7–136.4	113.6

caniniform teeth, inner row slightly enlarged, and one or two strong canines on each side of symphysis. Dentary with a row of large canines posteriorly, decreasing in size to small caniniform teeth at front of jaw. Vomer crescent-shaped, with one or two stout canines distally, a row of small canines crossing the head. Palatines with five or six large canines. Posterior nostril tubular, anterior nostril tubular with an elongate fleshy flap on posterior margin. Eye small and round. Umbraculum large, with a lobate margin. Pored lateral line scales with a single pore to exterior (Fig. 2).

Color in alcohol.—From the holotype except where indicated otherwise. Dorsum yellowish, with scattered, irregularly-shaped dark spots numerous on head, less abundant posteriorly. Top of head with numerous whitish spots, and some extending posteriorly on body in USNM 307398 (Fig. 3). Dorsal fin with alternating light and dark bands on anterior 3–4 spines, membranes hyaline. Fin rays of second dorsal-fin with light and dark bands, membranes hyaline. Upper pectoral-fin rays with series of small light spots that form seven or eight vertical bands, membranes hyaline. Pelvic and caudal fins with a series of dark blotches on rays, membranes hyaline.

Color of freshly frozen specimen.—The following description, provided by Dr. J. Barry Hutchins, was taken from WAM P24172-001, as it thawed from being freshly frozen. "Base red-brown with dark spots on head and back. Sides yellow-brown, with dark brown spots, ventral surface white. Dorsal fin hyaline with rays and spines spotted brownish-pink. Anal fin white with rays spotted orange. Pectoral rays spotted red-brown superiorly, inferiorly orange-brown. Ventrals orange-brown with faint brown-

Table 3.—Comparison of selected meristic characters in eleven species of *Platycephalus*. Means are shown in parentheses.

Species	Pored lateral line scales	Gill rakers	Dorsal-fin rays	Anal-fin rays
P. *arenarius*	69–83	3–4+9–12	13	13
P. bassensis	71–82	4–5+13–15	14	14
P. caeruleopunctatus	83–91	4–6+13–17	14	14
P. chauliodous	59–65 (63)	2+9–10	14	13
P. *endrachtensis*	67–81	1–2+6–9	13	13
P. fuscus	72–78	2–3+7–10	13	13
*P. indicus**	62–69 (65)	2–3+6–9	13	13
P. laevigatus	81–92	2+7–8	14	14–15
P. longispinis	70–82	5–7+14–19	14	14
P. marmoratus	64–70 (66)	2+7–9	13	13
P. speculator	80–93	3–4+10–12	14	14

* The status of *P. indicus* (Linnaeus, 1758) in Australian waters is unclear and data presented for that species are taken from Matsubara & Ochiai (1955).

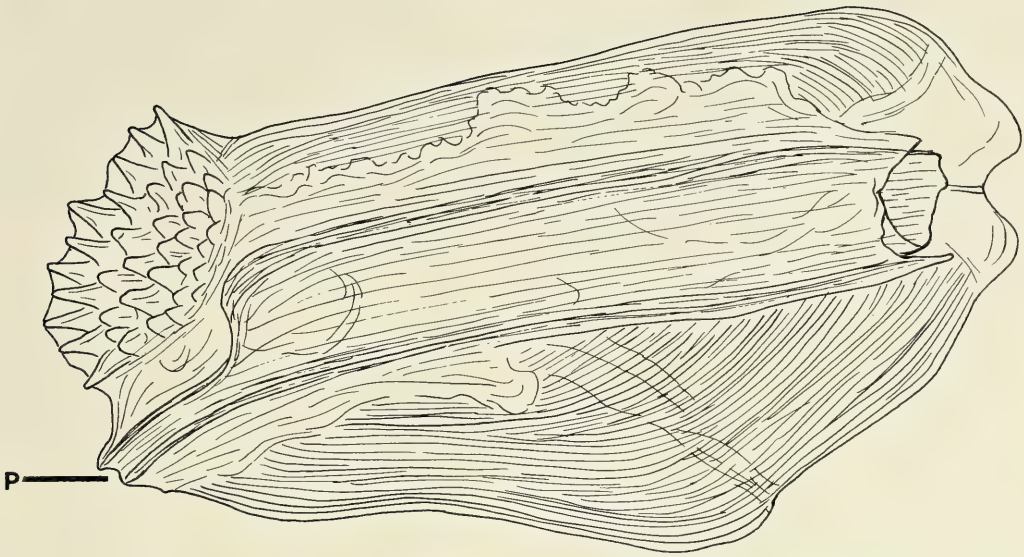


Fig. 2. Pored lateral line scale from *Platycephalus chauliodous,* AMNH 48856, paratype, 216 mm SL, 20th scale behind head, right side, scale 5.2 mm in length. Abbreviation: P-pore opening to exterior.

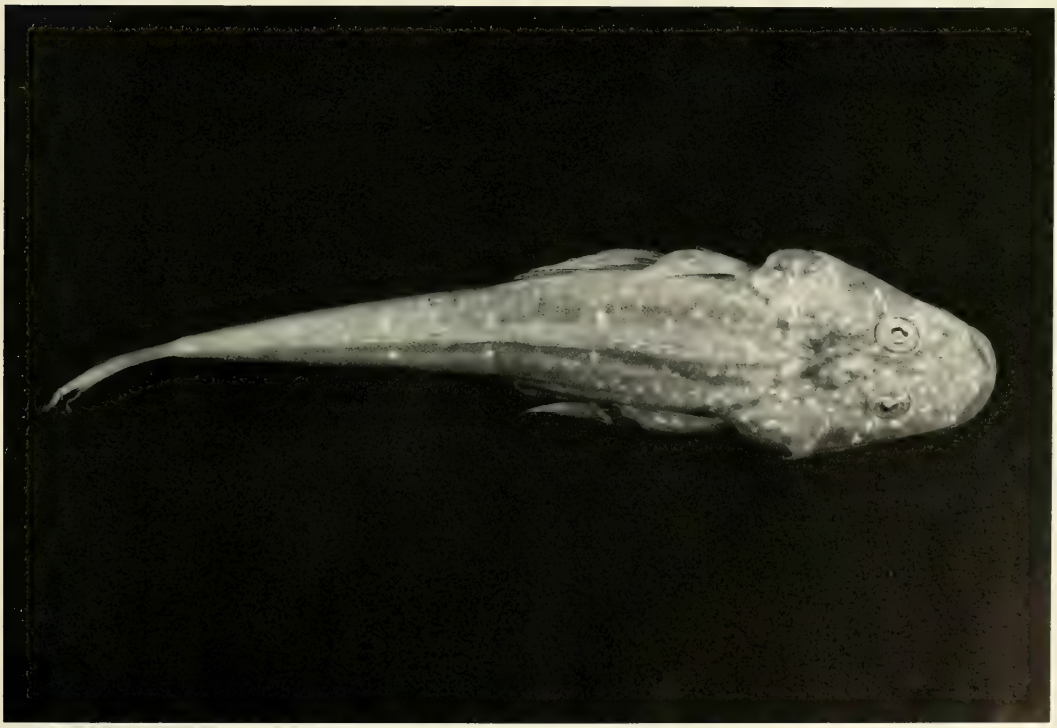


Fig. 3. *Platycephalus chauliodous,* USNM 307398, paratype, 77 mm SL, dorsal view.

green cross bars (approximately 8–9). Caudal-fin rays red-brown, hyaline connections. Cheeks ventrally bright yellow."

Distribution.—Infrequently taken at shallow coastal reefs from just north of Rottnest Island to Cape Freycinet, southern Western Australia (Hutchins & Swainston 1985).

Etymology.—The specific name *chauliodous,* from the Greek, in reference to the prominent canine teeth.

Remarks.—Comparison of *P. chauliodous* with the other ten species of *Platycephalus* is shown in Table 3. Although there is an overlap in number of pored lateral line scales with *P. marmoratus* and *P. indicus, P. chauliodous,* with a mean count of 63 has the lowest number of scales. It is the only member of the genus which usually has one fewer anal-fin rays than dorsal-fin rays. Occasional specimens may have one fin ray more or less than the usual number for that species but these are exceptional. Also, no other *Platycephalus* has large canine teeth positioned along the jaws (*P. indicus* has slightly enlarged teeth at the symphysis of the jaws). In life, the orange-red color of the dorsum is unique in the genus to *P. chauliodous.* Juvenile stages of *P. marmoratus* may have a brownish dorsum marbled with white but no reddish color is present.

Acknowledgments

I am greatly indebted to Dr. J. Barry Hutchins for calling my attention to the large specimen from Carnac I. and for providing color notes taken from that specimen. Thanks are due the following for making specimens available: Dr. Gareth Nelson (AMNH); Drs. Gerald R. Allen and J. Barry Hutchins (WAM); Drs. Kurt Deckert and Christine Karrer (ZMB); Dr. Martin F. Gomon (NMV); Dr. Barbara Herzig (NMW); Dr. Tomio Iwamoto (CAS); Dr. John R. Paxton (AMS); Dr. Barry C. Russell (NTM); Dr. Keith J. Sainsbury (CSIRO); Dr. William F. Smith-Vaniz, Eugenia B. Bohlke, and William G. Saul (ANSP); and Dr. Gerd von Wahlert (SMNS). The drawing of the holotype was skillfully prepared by Frances W. Zweifel and I am especially grateful to Dr. John R. Paxton and the Australian Museum for funding for drawing costs. The lateral line scale (Fig. 2) was drawn by Keiko H. Moore and Harold E. Dougherty took the photograph (Fig. 3).

Literature Cited

Bloch, M. E. 1795. Naturgeschichte der auslandischen Fische. J. Morino, Berlin 9:192 pp.

Castelnau, F. L. de. 1872. Contribution to the ichthyology of Australia. No. 1. The Melbourne fish market.—Proceedings of the Royal Zoological and Acclimatization Society of Victoria 1: 29–242.

Cuvier, G., & A. Valenciennes. 1829. Histoire naturelle des poissons. F. G. Levrault, Paris, 4: XXVI + 518 pp.

Hughes, D. R. 1981. Development and organization of the posterior field of ctenoid scales in the Platycephalidae.—Copeia 3:596–606.

Hutchins, B., & R. Swainston. 1985. Sea fishes of Southern Australia. Swainston Publishing, Perth, 180 pp., 678 pls.

———, & M. Thompson. 1983. The marine and estuarine fishes of Southwestern Australia. Western Australian Museum, 103 pp.

Klunzinger, C. B. 1872. Zur Fische-fauna von Süd-Australien.—Archiv fur Naturgeschichte 38(1): 17–47.

Knapp, L. W. 1973. *Platycephalus beauforti,* a new species of flathead (Pisces, Platycephalidae) from the Western Pacific.—Proceedings of the Biological Society of Washington 86(10):117–126.

———. 1987. New Australian fishes. Part 13. Two new species of Platycephalidae.—Memoirs of the Museum of Victoria 48(1):53–55.

Linnaeus, C. 1758. Systema nature per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentii, synonymis, locis. Tenth edition. Laurentius Salvius, Stockholm 1:1–824.

Macleay, W. 1885. Notices of new fishes.—Proceedings of the Linnean Society of New South Wales 9:170–172.

Matsubara, K., & A. Ochiai. 1955. A revision of the Japanese fishes of the family Platycephalidae (the flatheads).—Memoirs of the College of Agriculture, Kyoto University No. 68:109 pp., 33 figs., 3 pls.

May, J. L. 1986. Field guide to trawl fish from temperate waters of Australia. CSIRO, Hobart, 492 pp.

McCulloch, A. R. 1922. Checklist of the fish and fish-like animals of New South Wales. Part 3.—Australian Zoologist 2(3):86–130.

———. 1927. The fishes and fish-like animals of New South Wales. Royal Zoological Society of New South Wales, Sydney, 104 pp., 43 pls.

Quoy, J. R. C., & J. P. Gaimard. 1825. Remarques sur quelques poissons de mer. Pp. 182–401 *in* Louis de Freycinet, ed., Voyage autour du munde pendant 1817–1820. Pillet Aine, Paris.

Ramsay, E. P., & J. D. Ogilby. 1886. 2. Descriptions of some new or rare Australian fishes.—Proceedings of the Linnean Society of New South Wales (1)10(4):575–579.

Stead, D. G. 1908. New fishes from New South Wales. No. 1. New South Wales Government, Sydney, 12 pp.

Waite, E. R. 1921. Illustrated catalogue of the fishes of South Australia. Records of the South Australian Museum 2(1):208 pp.

———, & A. R. McCulloch. 1915. The fishes of the South Australian Government trawling cruise, 1914.—Transactions of the Royal Society of South Australia 39:455–476.

Oceanographic Sorting Center, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Appendix 1
Material of Other Species Examined

Neoplatycephalus aurimaculatus (Knapp, 1987): NMV 1404, 1 (290 mm), Tasmania, Bass Strait, 3 Feb 1981. AMS I.26328-001, 1 (333), Victoria, Bass Strait. NMV A3733, 2 (215–232), Victoria, Port Phillip Bay, 30 Mar 1971. USNM 280181, 1 (318), Bass Strait, Feb 1981. *Neoplatycephalus conatus* (Waite & McCulloch, 1915): AMS I.18710-007, 2 (160–174), Western Australia, off Point Culver, Feb 1976. AMS I.12393-94, 2 (226–236), South Australia, Investigator Strait. AMS I.13649, 1 (247), Great Australian Bight, west from meridian of Eucla, March 1912. AMS I.13650, 1 (268), same data as AMS I.13649. AMS I.12343, 1 (178), South Australia, Great Australian Bight. *Neoplatycephalus richardsoni* (Castelnau, 1872): AMS IB.507, 1 (442), Tasmania, Wineglass Bay. AMS IB.21166, 1 (248), Victoria, Lakes Entrance. NMV A1347, 1 (247), Tasmania, Bass Strait, 4 Nov 1980. *Platycephalus arenarius* Ramsey & Ogilby, 1886: AMS E.1581, 6 (81–102), Queensland, 22 mi SW Double Island point, 29 Jun 1910. AMS E.1581, 6 (81–102), Queensland, 22 mi SW Double Island point, 29 Jun 1910. AMS I.11033, 2 (189–225), Queensland, Wide Bay. WAM P25354-043, 1 (290), Western Australia, Monte Bello Islands, Apr 1975. *Platycephalus bassensis* Cuvier, *in* Cuvier & Valenciennes, 1829: NMV 11176, 1 (248), New South Wales, Port Jackson, 1864. AMS A.1342, 1 (230), Tasmania, Bass Strait, 3 Nov 1980. CAS 52596, 2 (202–223), South Australia, off Port Lincoln, 31 Dec 1982. AMS E.4600, 2 (318–328), Bass Strait between Gabo I. and Flinders I. *Platycephalus caeruleopunctatus* McCulloch, 1922: AMS I.15207-9, 3 (221–252), New South Wales, Shoalhaven R., 23 Nov 1913. AMS I.15204-6, 3 (175–288), New South Wales, Lake Illawara, 3 Nov 1913. AMS I. 20720-002, 1 (308), New South Wales, NW Solitary I., 30 Jun 1978. AMS I.10655, 1 (275), Lord Howe I. *Platycephalus endrachtensis* Quoy & Gaimard, 1825: AMS I.20751-005, 1 (382), Queensland, Lizard I., 8 Feb 1979. NTM S.10166-001, 1 (114), Northern Territory, Shoal Bay, 7 Aug 1974. NTM S.10169-002, 2 (83–103), Northern Territory, Shoal Bay, 16 Aug 1972. USNM 306476, 8 (195–297), Queensland, Gulf of Carpenteria, 4 Jun 1979. *Platycephalus fuscus* Cuvier, *in* Cuvier & Valenciennes, 1829: AMS I.20538-001, 2 (203–225), New South Wales, Sydney harbour, 27 Apr 1977. AMS I.16475-001, 1 (234), New South Wales, Smith Lake, 21–26 May 1972. CAS-SU 13045, 1 (293), Queensland, Brisbane R. AMS I.21282-007, 2 (205–214), Queensland, near Halftide, 28 Sept 1979. CAS-SU 20956, 2 (290–295), New South Wales, Port Jackson. *Platycephalus laevigatus* Cuvier, *in* Cuvier & Valenciennes, 1829: AMS I.7543-4, 2 (271–277), Victoria, Melbourne Market, Nov 1905. ZMB 5353, 1 (190), South Australia, Adelaide. SMNS 2245, 2326, 3 (305–355), Victoria, Melbourne, Hobson Bay, 1877. AMS I.19676-001-2, 2 (384–395), New South Wales, Merimbula Bay, 18 Mar 1976. *Platycephalus longispinis* Macleay, 1884: AMS I.20194-015, 6 (162–240), South Australia, Investigator Strait, 14 Mar 1978. AMS I.19832-001, 2 (193–210), New South Wales, off Whale Beach, 10 Oct 1976. ANSP 98673, Queensland, off Point Lookout, 29 Oct 1951. *Platycephalus marmoratus* Stead, 1908: WAM P2745-001, 2 (268–335), Western Australia, off Rottnest I., 30 Dec 1981. WAM P22098-001, 1 (255), Western Australia, Cape Cuvier, 29 Jul 1972. AMS I.18756-001, 1 (330), New South Wales, off Broken Bay. AMS 20870-001, 1 (155), New South Wales, Bondi Beach near Sydney, 30 Oct 1977. AMS I.3608, 1 (218), Tasmania, Flinders I., Feb 1914. *Platycephalus speculator* Klunzinger, 1872: SMNS 1570, 1 (259), Victoria, Hobson Bay, 1868. CSIRO C4296, 1 (269), Western Australia, Cheynes Beach, 25 Mar 1974. WAM P22220-001, 1 (251), Western Australia, Pallinup, Marlboro Point. AMS I.16354-001, 1 (280), Western Australia, King George's Sound. AMS IB.2701, 1 (145), Western Australia, Starvation Boat Harbour. AMS I.20180-048, 5 (29–160), South Australia, Kangaroo I.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 30–39

ON *PARACALOCARIS SAGAMIENSIS,* A NEW GENUS AND SPECIES FROM JAPAN (DECAPODA: THALASSINIDEA: AXIIDAE)

Katsushi Sakai

Abstract.—A new genus and species of the family Axiidae, *Paracalocaris sagamiensis,* collected from Sagami Bay, Japan, and previously reported as *Calocaris* (*Calocaris*) *granulosa* Grebenyuk, is described. *P. sagamiensis* cannot be placed in either *Calocaris* or *Lophaxius* based on the eye, as it is triangular with dorsally upraised, unpigmented cornea, on the unarmed anterolateral margin of the carapace, and on the 2-segmented pleopod 1, with the distal segment distally trilobed. *Calocaris* (*Calocaris*) *granulosa* is transferred to the new genus, and along with *P. sagamiensis,* placed in the family Axiidae.

From among the material of deep-sea Decapoda Crustacea collected in crab traps by H. Ikeda of Hayama Municipal Museum, Japan, a most interesting axiid specimen was kindly sent to me for study. This specimen, though closely related to *Calocaris* (*Calocaris*) *granulosa* Grebenyuk, from Alaska, differs in various points, and is described as *Paracalocaris sagamiensis* new genus and species. *Calocaris* (*Calocaris*) *granulosa* is transferred to the new genus, and along with *P. sagamiensis,* placed in the family Axiidae.

The following abbreviations are used in this paper; CL, carapace length including rostrum; TL, total length of body; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, W. Germany.

Family Axiidae Huxley, 1878

Paracalocaris, new genus

Diagnosis.—Hermaphroditic. Carapace with anterolateral margin unarmed; postcervical carina entire. Rostrum elongate, at distinctly lower level than anterior carapace; rostral margins armed. Median carina entire; submedian carina absent; lateral carina extending only short distance posterior to rostrum, armed with one or two spines. Eyestalk not mesially contiguous; cornea unpigmented, upraised or not. Antennal acicle short, situated mesial to dorsodistal spine of segment 2. Maxillipeds 1–3 with exopods and epipods; small podobranch on maxilliped 2; large podobranch on maxilliped 3.

Pereopods lacking exopods; epipods on pereopods 1–4; large podobranch on pereopods 1–3; pleurobranchs absent. Pereopod 1 with chelae subequal; anterior margin of palm armed. Pereopod 2 chelate.

Pleopod 1 2-segmented, distal segment expanded, distally trilobed, with patch of hooks on mesiodistal lobe. Pleopod 2 with endopod lacking distal portion, slender appendix masculina of single article, with appendix interna articulating at its base.

Telson longer than wide, with two dorsal rows of non-articulating spines. Uropodal exopod with transverse suture.

Etymology.—The generic name is derived from the Greek "para," a prefix meaning "near," plus the generic name "*Calocaris.*" Gender: feminine.

Type species.—*Paracalocaris sagamiensis,* new species.

Species included.—*Paracalocaris saga-*

miensis, new species, and *Calocaris* (*Calocaris*) *granulosa* Grebenyuk, 1975.

Remarks.—The present new genus *Paracalocaris* is similar to *Calocaris* Bell, 1853, and *Lophaxius* Kensley, 1989, in being hermaphroditic, and having a post-cervical carina on the carapace; the pleopod 2 with a slender appendix masculina and a free appendix interna (Fig. 5D); and lacking pleurobranchs on thoracic somites 2–4. However, *Paracalocaris* differs in several characters from *Calocaris* and *Lophaxius.* In *Calocaris,* as exemplified by its type species, *C. macandreae* Bell, 1853, the anterolateral margin of the carapace has a spine; the eyes are mesially contiguous; the antennal acicle is reduced; the maxilliped 2 bears a reduced podobranch with a few gill filaments; and pleopod 1 (Fig. 5C) consists of two segments, the distal segment being expanded in the form of a lobe, and with a patch of hooks on small mid-terminal margin. In *Paracalocaris,* the anterolateral margin of the carapace is unarmed; the eyes are not mesially contiguous; the antennal acicle is short; the maxilliped 2 has a large podobranch; and the pleopod 1 is made of two segments, the distal segment being expanded, trilobed, and with patch of hooks on mesial lobe (Fig. 5A). In *Lophaxius* the eyes are not mesially contiguous; the antennal acicle is short; and the maxilliped 2 has a large podobranch (Kensley 1989:962), as in *Paracalocaris.* However, *Lophaxius* differs from *Paracalocaris* and *Calocaris,* in that the anterolateral margin of the carapace has a spine; the pereopod 2 is subchelate; and the pleopod 1 consists of two segments, the distal segment being spatulate with a small mesial patch of hooks (Kensley 1989:962).

Grebenyuk's species, *Calocaris* (*Calocaris*) *granulosa* is also placed in *Paracalocaris.* This species has a small antennal acicle; the eyestalk is flattened, but the cornea is not upraised as *P. sagamiensis*; and pleopod 1 is 2-segmented, the distal segment being distally trilobed (Grebenyuk 1975: figs. 1–5).

Paracalocaris is here treated under the family Axiidae following Sakai & de Saint Laurent (1989:11).

Paracalocaris sagamiensis, new species
Figs. 1–5

Calocaris (*Calocaris*) *granulosus.*—Sakai, 1987:300.

Material examined.—1 ♀, holotype, TL = 81 mm, CL = 31 mm, USNM 231420, off Ohiso, Sagami Bay, Japan, 250–280 m, crab trap, 3 Apr 1984; H. Ikeda, coll.

Diagnosis.—Hermaphroditic. Rostrum styliform, with three marginal spines, margins shortly extending posteriorly onto gastric region; lacking submedian carina, but with post-cervical carina on carapace. Eye triangular with obtuse tip, bearing upraised cornea without pigments. Pereopods 1 subequal, palm with dorsal row of prominent spines; pereopod 3 with propodus elongate, ventrolaterally without transverse rows of spines. Pleurobranchs absent. Pleopod 1 composed of two segments, distal one distally trilobed.

Description.—Hermaphroditic, Rostrum (Fig. 1A, B) styliform, with three marginal spines; tip acute. Carapace compressed, with scattered rounded tubercles; anterolateral margin unarmed. Cervical groove dorsally distinct, ventrolaterally indistinct. Gastric region anteriorly arched to rostrum, lateral carina short, with strong spine, anteriorly continuous with lateral margin of rostrum; submedian carina absent; median carina extending from base of rostrum to posterior margin of carapace, armed with median tubercles.

Eye peduncles (Fig. 1C) small, thick, less than one-fourth length of rostrum, distally triangular with obtuse tip; cornea small, poorly defined, not pigmented, upraised. Antennular peduncle slightly shorter than rostrum; segment 1 as long as segments 2 and 3 combined, its dorsal surface medially concave in proximal half to accommodate eye; dorsolateral flagellum 23 mm long,

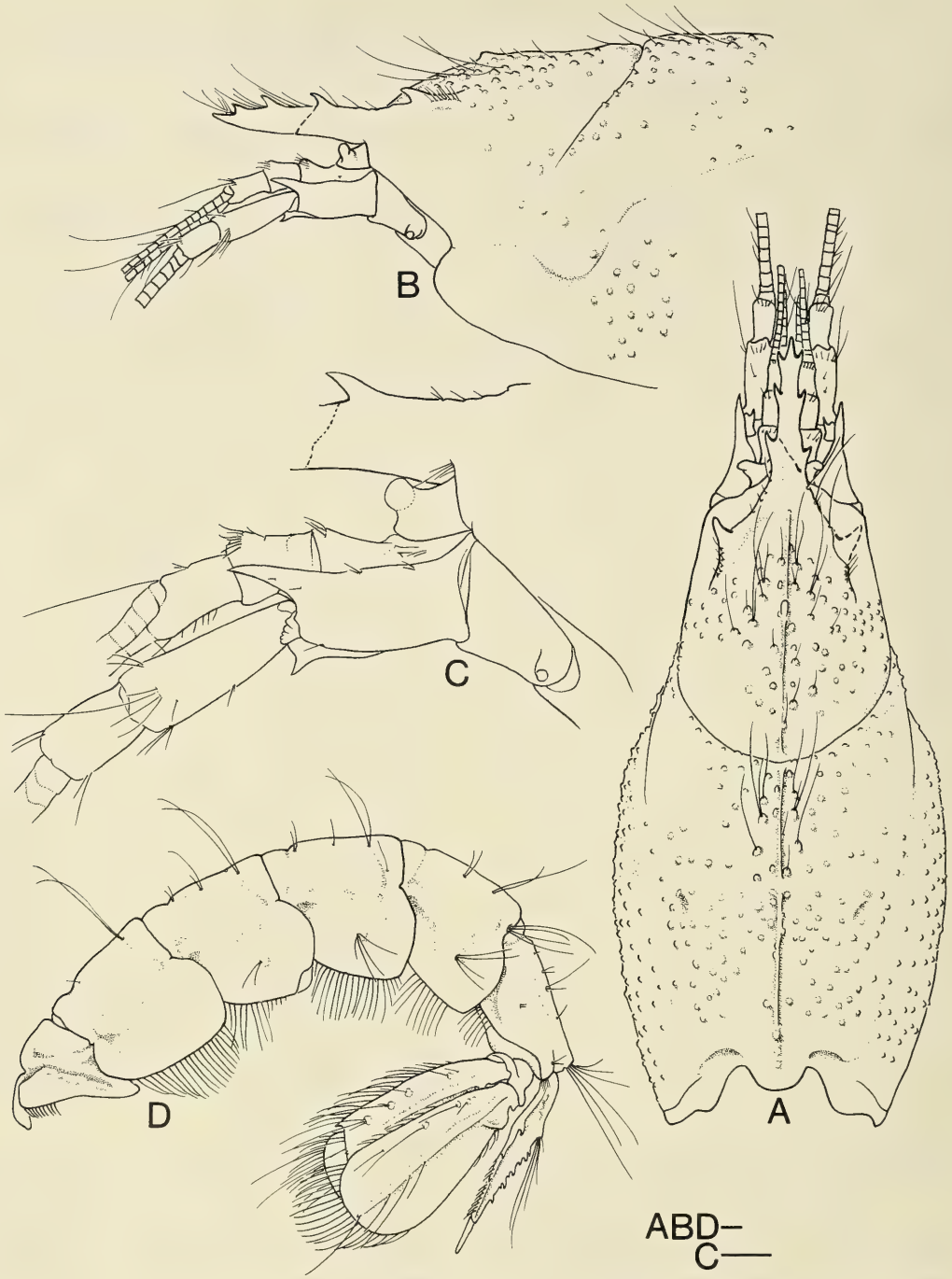


Fig. 1. *Paracalocaris sagamiensis,* new species, ♀, holotype. A, carapace and cephalic appendages, dorsal view; B, anterior carapace, lateral view; C, antennule, antenna, and eyestalk, lateral view; D, abdomen and tail-fan, lateral view. Scales equal 1 mm.

ventromesial flagellum 34 mm long. Antennal peduncle overreaching antennular peduncle by segment 5; segment 1 unarmed; dorsodistal spine of segment 2 well developed, directed anteriorly, extending to about proximal third of segment 4; antennal acicle small, distinctly shorter than, and situated mesial to dorsodistal spine of segment 2; ventrodistal spine of segment 3 short; segment 4 about as long as segment 2, twice length of segment 5, flagellum measuring 63 mm.

Mandible with 3-segmented palp. Maxillular palp (Fig. 2A) 2-segmented, distal segment about as long as proximal one, proximally sinuous with two terminal setae. Maxilla with long posterior flagellum on scaphognathite (Fig. 2B); palp distally tapering, curved mesially. Maxilliped 1 (Fig. 2C) with 2-segmented palp extending to level of distal margin of endite; distal process of exopod consisting of two subequal segments. Maxilliped 2 with proximal segment and flagellum on exopod; epipod leaf-like, with simple rudimentary podobranch and arthrobranch lacking gill-filaments. Maxilliped 3 (Fig. 4D, E) with coxa unarmed; basis with mesial denticle; ischium with denticulate crest on mesial margin widely separated by broad concavity from posterior margin with three well-spaced denticles; merus slightly shorter than ischium, with 3–4 teeth on posterior margin, distal one very distinct, others small; carpus about ¾ length of merus, with ventrodistal spine; propodus about ⅘ length of carpus, dactylus about ⅘ length of propodus.

Pereopods 1 subequal, chelae vertically positioned.

Left, larger cheliped (Fig. 3A) with coxa (not figured) provided with two spines on posteromesial surface, and with seven denticles on lateral margin. Basis (not figured) with obtuse spine on mesial margin. Ischium with three sharp spines on posterior margin. Merus about 2.3 times as long as broad; anterior margin with two sharp subdistal spines and four tubercles; ventral margin with four sharp equidistant spines, and outer surface with sharp distal spine near articulation. Carpus triangular, less than half length of merus, armed with three sharp proximal and two small distal spines on dorsal margin. Chela about 3.5 times as long as carpus; palm about as long as wide, increasing in width distally; anterior margin with four sharp distally directed spines, and obtuse spine proximally; posterior surface with proximally broad but distally narrow carina along entire length of surface, bearing lateral row of six distinct, outwardly directed spines and mesial row of nine denticles on proximal third; lateral and mesial surfaces provided with granules with tuft of setae. Dactyl about 1.3 times as long as palm; cutting edge largely gaping proximally with a broad tooth in midlength, and armed with row of obtuse denticles on distal half; lateral and mesial surfaces medially carinate. Cutting edge of fixed finger largely convex and denticulate.

Right, smaller cheliped (Fig. 3B), similar to, but less wide and more denticulate than left. Coxa and basis as in larger cheliped. Ischium armed with five sharp spines on posterior margin. Merus smaller than that of larger cheliped, about 2.3 times as long as broad; anterior margin armed with two sharp subterminal spines, posterior margin with row of nine sharp spines, and lateral surface with sharp distal spine near articulation. Carpus less than half length of merus; anterior margin with four spines, middle two the largest. Chela more than three times as long as carpus; palm less wide than that of left cheliped, with six sharp spines directed anteriorly; posterior surface showing distinct carina as in larger cheliped, carina triangular on proximal third, laterally with nine distinct tubercles or spines, and mesially with 12 tubercles, becoming narrow in distal ⅔; lateral and mesial surfaces furnished with granules, each having tuft of setae. Dactyl about 1.3 times as long as palm;

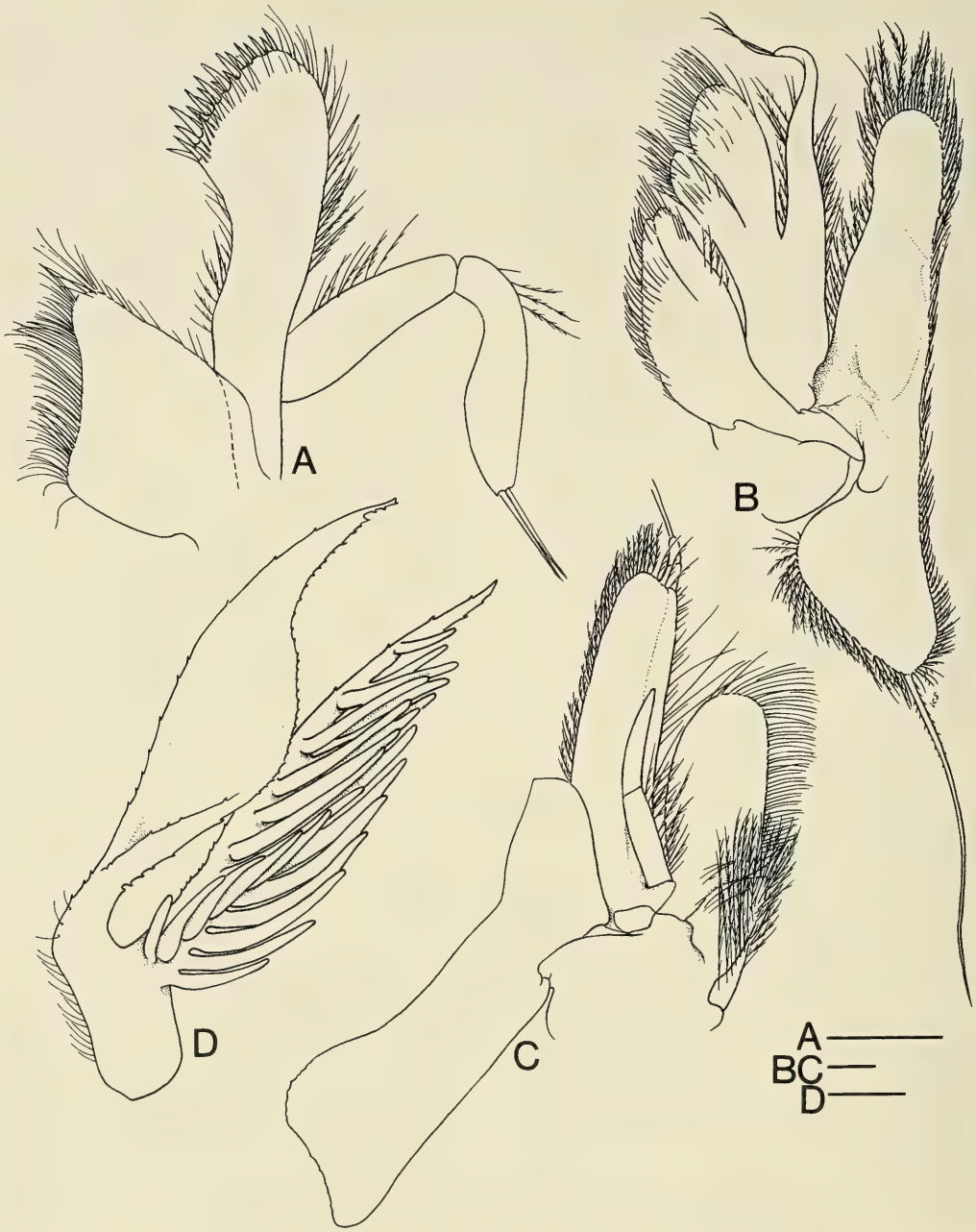


Fig. 2. *Paracalocaris sagamiensis,* new species, ♀, holotype. A, maxillule, external face; B, maxilla, external face; C, 1st maxilliped, internal face; D, epipod and podobranch of 2nd pereopod. Scales equal 1 mm.

cutting edge largely gaping proximally, with broad tooth at about midlength, concave with row of denticles on distal half. Fixed finger similar to that of larger cheliped.

Pereopod 2 with coxa having proximal spine on each posteromesial and anteromesial surfaces, and with group of seven denticles proximally on lateral margin. Basis

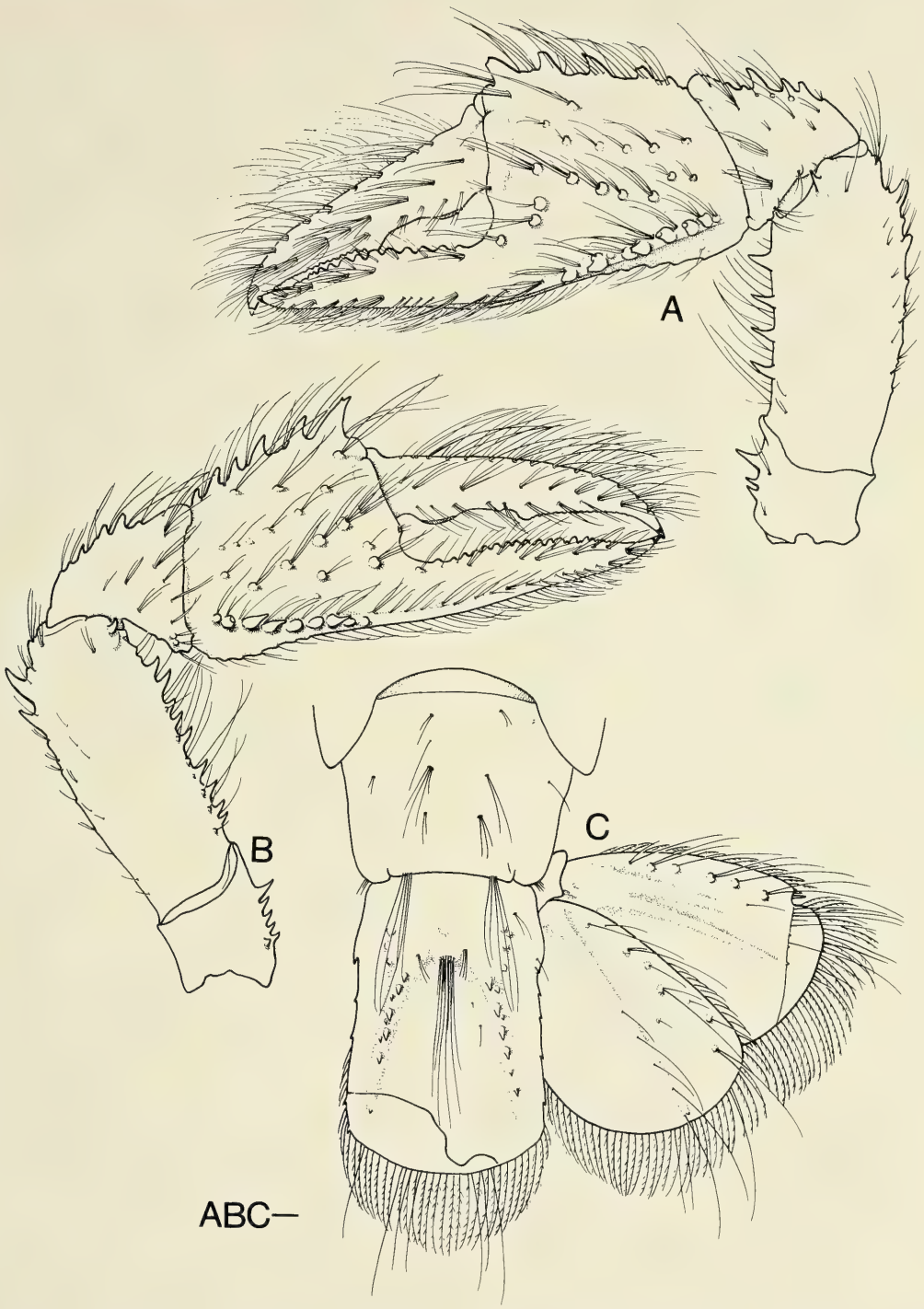


Fig. 3. *Paracalocaris sagamiensis,* new species, ♀, holotype. A, 1st larger pereopod, left side; B, 1st smaller pereopod, right side; C, tail-fan, dorsal view. Scales equal 1 mm.

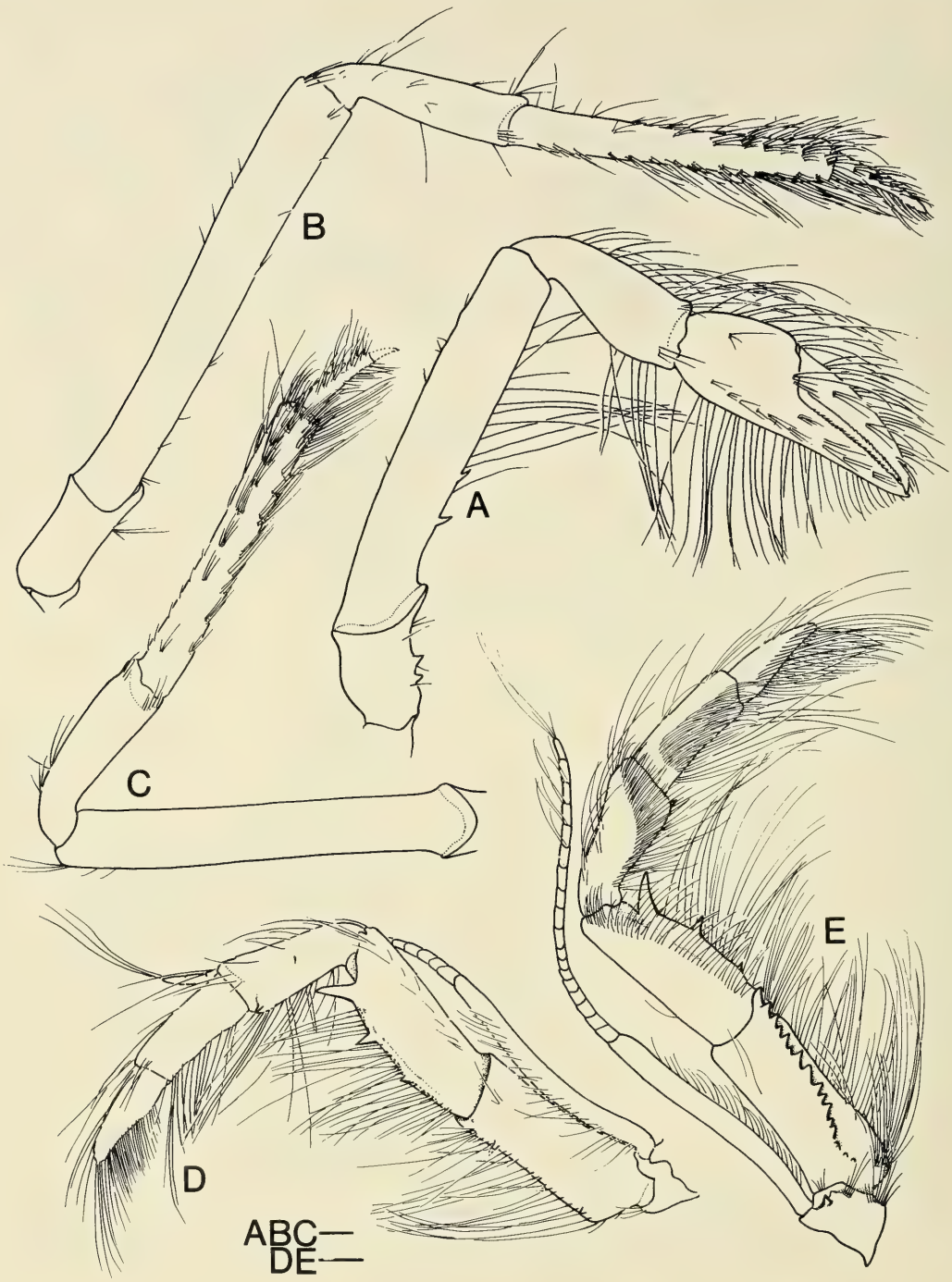


Fig. 4. *Paracalocaris sagamiensis,* new species, ♀, holotype. A, 2nd pereopod, right side; B, 3rd pereopod, right side; C, 4th pereopod, right side; D, 3rd maxilliped, interior face; E, 3rd maxilliped, mesial view. Scales equal 1 mm.

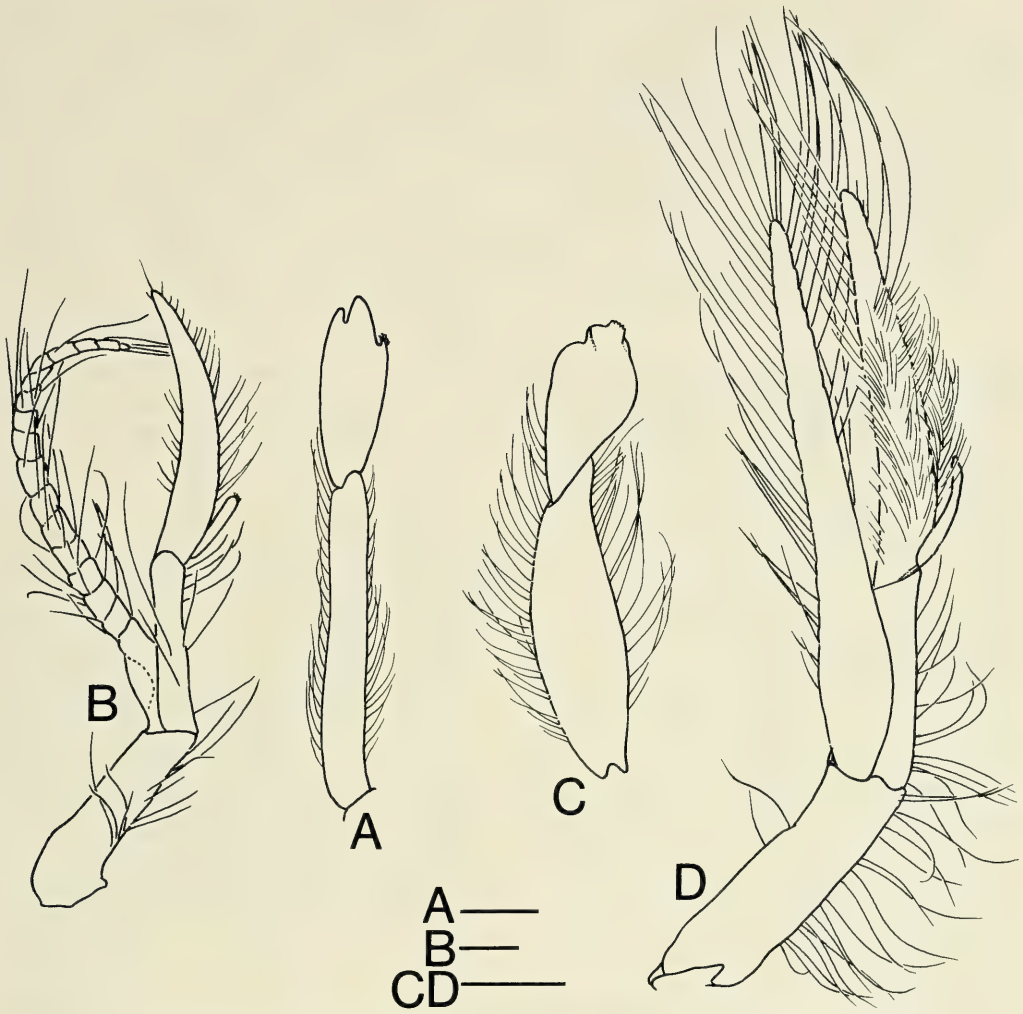


Fig. 5. A, B, *Paracalocaris sagamiensis,* new species, ♀, holotype: A, 1st left pleopod, anterior view; B, 2nd right pleopod, mesial view. C, D, *Calocaris macandreae* Bell, ♀, SMF 12810, from North Sea (58°10.2′N, 05°32′6E–58°11.7′N, 05°29.9′E, 98 m): C, 1st left pleopod, anterior view; D, 2nd pleopod, anterior view. Scales equal 1 mm.

unarmed, ischium (Fig. 4A) with two posterior spines. Merus about four times length of ischium, with two posterior spines on proximal half. Carpus about half length of merus, unarmed. Chela about 1.5 times as long as carpus; cutting edges of dactylus and fixed finger armed with fine distally directed spines. Pereopod 3 with coxa having genital pore, and with proximal spine on anteromesial surface of left side, but unarmed on right side, and with group of five denticles proximally on lateral margin. Basis unarmed. Ischium (Fig. 4B) slender, unarmed. Merus about four times as long as ischium, unarmed. Carpus about ⅔ length of merus. Propodus about twice as long as carpus, ventrolaterally with row of tufts of setae. Pereopod 4 with coxa having two spines on anteromesial margin. Basis and ischium unarmed. Merus (Fig. 4C) elongate, distinctly

Table 1.—Branchial formula of *Paracalocaris sagamiensis*, new species (r = rudimentary, having no gill-filaments).

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Epipods	1	1	1	1	1	1	1	—
Podobranchs	—	r	1	1	1	1	—	—
Arthrobranchs	—	r	2	2	2	2	2	—
Pleurobranchs	—	—	—	—	—	—	—	—

shorter than that of pereopod 3. Carpus about half length of merus. Propodus more than 1.5 times as long as merus, ventrolaterally with row of tufts of setae. Pereopod 5 with coxa having genital pore, unarmed. Gill filaments simple and small in number (Fig. 2D).

Abdomen (Fig. 1D) unarmed; length ratio of abdominal somites 1–6 to abdominal somite 2 as follows: 0.7; 1; 1; 1.1; 1.1; 1.2. Pleuron 1 narrow, ventral margin obtuse, pleura 2–5 broad, ventrally truncate. Pleopod 1 (Fig. 5A) 2-segmented; distal segment about half length of proximal one, distally trilobed, middle lobe larger than lateral ones. Pleopod 2–5 (Fig. 5B) narrow, and biramous; endopod 2-segmented with free appendix interna, distal segment sickle-shaped, and about 1.5 times as long as proximal segment; exopod multiarticulate.

Telson (Fig. 3C) about 1.6 times as long as broad, about 1.3 times as long as abdominal somite 6, not quite reaching level of posterior margin of uropodal endopod; lateral margin slightly convex proximally with spine at anterior third, and with four well-spaced denticles on posterior ⅔; posterior margin semicircular, unarmed; dorsal surface with transverse tuft of setae at about anterior third, and diagonal row of 8–9 denticles on each side extending posteriorly near posterolateral angle. Uropodal exopod broad; lateral margin largely convex; dorsal surface with smooth outer and inner ribs, and row of few tubercles each having setae directed parallel to lateral margin; distal transverse suture with few denticles. Uropodal endopod broad; outer margin unarmed; dorsal surface with smooth mid-rib, and few tubercles on outer half.

Remarks.—The present new species from Sagami Bay is similar to *Paracalocaris granulosa* (Grebenyuk, 1975) from Alaska, in being hermaphroditic, having short antennal acicles, the post-cervical carina on the carapace, and the shape of the tail fan and 1st pereopod, but differs in other details.

In *P. sagamiensis,* the rostrum is styliform with three marginal spines; the eye is less than one-fourth the length of the rostrum, and the cornea is upraised to form a rounded, dorsolateral protrusion; the antennular peduncle is slightly shorter than the rostrum, and its proximal segment is unarmed; the abdominal somite 6 is longitudinally furnished with two rows of 4–5 tufts of setae; the telson is slightly shorter than the uropod, armed with an anterior spine and four denticles on the lateral margin, and with a semicircular posterior margin; and the uropodal exopod is unarmed on the lateral margin. In pereopod 1, the ischium is provided with three (larger cheliped) or seven (smaller cheliped) spines on the posterior margin, the merus with four (larger cheliped) or nine (smaller cheliped) spines on the posterior margin, and the palm with 5–6 spines on the anterior margin.

In *P. granulosa,* the rostrum is an elongate triangle with one marginal spine; the eye is elongate and one-third the length of the rostrum, with the cornea not upraised; the antennular peduncle overreaches the rostrum by the distal half of the terminal segment,

the proximal segment is armed with three denticles; the abdominal segment 6 is dorsally provided with two rows of six tufts of setae (Grebenyuk 1975: fig. 1–8); the telson is slightly longer than the uropod, armed with three denticles on the lateral margin, and is slightly concave on the posterior margin; and, the uropodal exopod is armed with three spines on the outer margin. In pereopod 1 the ischium is furnished with two spines on the posterior margin, the merus with seven spines on the posterior margin, and the palm with a row of four spines on the anterior margin (Grebenyuk 1975:299).

Acknowledgments

I am much indebted to Mr. H. Ikeda of Hayama Municipal Museum, Japan, who allowed me to examine this interesting specimen, and also Dr. M. Türkay of Senckenberg Museum, Frankfurt am Main, who kindly prepared referencial material and literature. Thanks are due to Drs. R. B. Manning and R. Lemaitre of the Smithsonian Institution, Washington D.C., for their comments and improvements to the manuscript, and also to Mrs. Terumi Nakano of Tokushima, who drew parts of figures for this paper.

Literature Cited

Bell, T. 1853. A history of the British stalk-eyed crustacea. John Van Voorst, London, lxv, 386 pp., 147 figs.

Grebenyuk, L. P. 1975. Two new decapoda species of the superfamily Thalassinidea.—Zoologichesky Zhurnal 54(2):299–304 (In Russian with English summary).

Huxley, T. H. 1878. On the classification and the distribution of the crayfishes.—Proceedings of the Zoological Society of London 1878:752–788.

Kensley, B 1989. New genera in the thalassinidean families Calocarididae and Axiidae (Crustacea: Decapoda).—Proceedings of the Biological Society of Washington 102:960–967.

Sakai, K. 1987. Two new Thalassinidea (Crustacea: Decapoda) from Japan, with the biogeographical distribution of the Japanese Thalassinidea.—Bulletin of Marine Science 41(2):296–308.

———, & M. de Saint Laurent. 1989. A check list of Axiidae (Decapoda, Crustacea, Thalassinidea, Anomura), with remarks and in addition descriptions of one new subfamily, eleven new genera and two new species.—Naturalists, Tokushima 3:1–104.

Tokushima Biological Laboratory, Shikoku Women's University, Tokushima, 771-11, Japan.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 40–48

PONTONIINE SHRIMPS (DECAPODA: CARIDEA: PALAEMONIDAE) OF THE NORTHWEST ATLANTIC. II. *PERICLIMENES PATAE*, NEW SPECIES, A GORGONIAN ASSOCIATE FROM SHALLOW REEF AREAS OFF THE TURKS AND CAICOS ISLANDS AND FLORIDA KEYS

Richard W. Heard and Stephen Spotte

Abstract.—*Periclimenes patae,* a small pontoniine shrimp associated with shallow-water gorgonians, occurs at depths of usually less than 12 m on the fringing reef off Pine Cay in the Turks and Caicos Islands and off Looe Key in the Florida Keys. This new species appears to be most closely related to *P. iridescens* Lebour, 1949, described originally from Bermuda. *Periclimenes patae* can be separated from the holotype of *P. iridescens* by fewer rostral teeth, second pereopods equal or nearly equal in size, chelae of second pereopods lacking distinct teeth, dactyls of pereopods 3–5 entire (not bifid), and a nearly transparent body in life. There is confusion over the previous northwestern Atlantic records for *P. iridescens* from Venezuela, Colombia, Curaçao, Gulf of Mexico, and east coast of the United States. Our observations and research indicate the existence of at least three additional undescribed species within the "iridescens" complex from the western North Atlantic.

This report is the second in a series devoted to the taxonomy, distribution, and ecology of shrimps belonging to the palaemonid subfamily Pontoniinae. The first report (Heard 1986) dealt with the taxonomy of the genus *Neopontonides* Holthuis, 1951.

During April 1988, an undescribed species of *Periclimenes* Costa, was discovered living on gorgonians along the shallow (1–12 m) areas of the fringing reef off Pine Cay, Turks and Caicos Islands (British West Indies). Additional specimens of this species, which were collected off Looe Key in the Florida Keys, were made available to us through the courtesy of Brian Kensley of the National Museum of Natural History. The new species, which most closely resembles *P. iridescens* Lebour, 1949, is described in this report.

The holotype and part of the paratype series are in the collections of the National Museum of Natural History (USNM). Other paratypes have been deposited in the collections of the British Museum (BMNH), Gulf Coast Research Laboratory Museum (GCRL), and Los Angeles County Museum (LACM). Additional specimens have been deposited in the collections of the USNM, and the Marine Environmental Sciences Consortium Museum (MESC), Dauphin Island, Alabama. Additional non-type material has been deposited in the National Museum of Natural History (USNM 252164). The abbreviation CL stands for carapace length, which was measured from the tip of the rostrum to the posterodorsal margin of the carapace.

Periclimenes patae, new species
Figs. 1–4

Material examined.—Fringing reef northwest of Pine Cay, Turks and Caicos Islands, British West Indies (near 21°53'N,

072°05'W): Holotype ♀ (ovigerous, CL 3.8 mm), USNM 252162, on gorgonian, depth 3–4 m, J. A. McLelland (coll.), 18 Nov 1989.—Paratypes: 12 ♀ (ovigerous, CL 3.3–4.2 mm), 12 ♂ (CL 2.6–3.2 mm), USNM 252163, same collection data as holotype.—5 ♀ (ovigerous), 2 ♀, GCRL 1139, same collection data as holotype.—2 ♀ (ovigerous), 2 ♂, BMNH 1990:28:4, on gorgonians, depth 3–4 m, J. A. McLelland (coll.), 17 Nov 1989.—3 ♀ (2 ovigerous), 1 ♂, LACM 88-124.1, on gorgonians, depth 7–8 m, J. A. McLelland (coll.), 16 Nov 1989.—8 ♀ (3 ovigerous), 5 ♂, MESC 6179-10589, on gorgonians, depth 9–10 m, J. A. McLelland (coll.), 19 Nov 1989.—1 ♀ (CL 4.0 mm), illustrated and in collection of RWH, on gorgonian, depth 9–10 m, R. W. Heard (coll.), 12 Apr 1989.—1 ♀ (ovigerous), in collection of RWH, from the gorgonian *Pseudopterogorgia americana* (Gmelin), depth 12 m, S. Spotte/P. M. Bubucis (coll.), 14 Apr 1989.—3 ♀ (2 ovigerous), 4 ♂, GCRL 1140, on gorgonians, depth 4–5 m, J. A. McLelland (coll.), 10 Nov 1989.

Looe Key, Florida Keys, Florida: 3 ♀ (ovigerous), 2 ♂, USNM 252161, poison station #24, upper spur and groove, vertical buttress wall (gorgonians present), 5–6 m, B. Kensley and M. Schotte (coll.), 27 Jan 1983.

Diagnosis.—Small (CL 2.2–4.2 mm), transparent in life. Rostrum nearly straight or curved slightly upward at tip, reaching anteriorly to midregion of second segment of antennular peduncle; 3–6 dorsal teeth, usually 4 in males and 5 in females; often 1, rarely 2, small vestigial anteroventral teeth on larger specimens. Carapace with well developed antennal and hepatic spines, but without postorbital ridge, other spines, or ornamentation. Abdominal pleura broadly rounded; sixth abdominal somite twice as long as fifth. Posterior tip of telson having mesial spines ¾ length of intermediate spines. Cornea of eye as broad as eyestalk, constricted at junction with eyestalk; accessory pigment spot and associated ommatidia present on dorsoproximal margin of cornea. Pereopods 2 equal or subequal in size and development, chelae lacking distinct teeth. Pereopods 3–5 with dactyls entire (not bifid or biunguiculate), propodi having single spine-like seta on distoflexor margin, propodus of pereopod 5 with single row of comb setae on distal margin. Eggs, depending on stage of development, with maximum diameter of 0.5 (undeveloped) to 0.7 mm (hatching stage). Ovigerous females with 10–35 eggs.

Description.—Female: Rostrum (Figs. 1, 4e–h) nearly straight or slightly curved upward at tip, reaching anteriorly to midregion of second segment of antennular peduncle; dorsal surface with 4–6 spines interspersed with setae; second spine on carapace usually even with, or anterior to, orbital margin; posterior tooth distinctly behind orbital margin; ventral surface with several setae in mid-region, occasionally armed with single, small, vestigial tooth near tip, weakly developed lateral carinae present posteriorly. Antennal spine weakly buttressed, well developed, acute, attenuated. Hepatic spine well developed, slightly larger, more robust, and less attenuated than antennal spine. Carapace without postorbital ridge, or other ornamentation or spines. Abdominal pleura broadly rounded; sixth abdominal somite twice as long as fifth but same length as telson, as measured along mid-dorsal surface. Telson (Fig. 3i) with 2 pairs of dorsolateral spines, anterior pair distal to mid-length of segment, posterior pair closer to anterior pair than to end of telson; 3 pairs of apical spines present, lateral spines short, medial (setose) spines three-fourths length of intermediate spines; minute, acute process at apex between medial spines.

Cornea of eye as broad as eyestalk, constricted at junction with eyestalk; accessory pigment spot and associated ommatidia present on dorsoproximal margin of cornea. Antennular peduncle with sharp, slender stylocerite not extending to midline of basal segment; distolateral margin of basal seg-

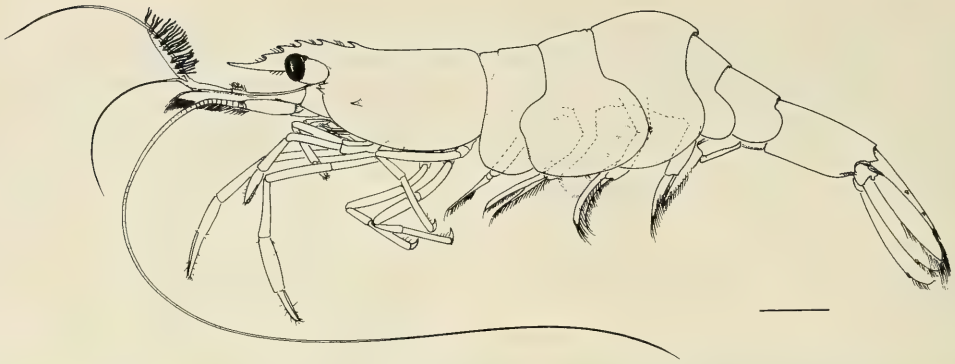


Fig. 1. *Periclimenes patae,* new species, lateral view of holotype (ovigerous female). Right antennule, antenna, and pereopods 3–5 not shown. Scale equals 1.0 mm.

ment with single spine; combined length of second and third segments shorter than basal segment. Lateral antennular flagellum with two branches fused for approximately five joints; extended part of shorter branch consisting of approximately three joints and shorter than fused portion; 6–10 small clusters of aesthetascs present. Antennal scale overreaching antennular peduncle, length ⅓ greater than width, lateral margin nearly straight, distolateral spine not extending to anteromesial angle of blade. Antennal peduncle extending past midpoint of blade; basal segment with lateral spine.

Mandible lacking palp, incisor process ending in 4 distinct teeth, molar process dentate with numerous small spine setae; distal tooth of incisor distinctly larger than the rest. Maxilla 1 with upper endite (lacinia) bearing 5–6 stout apical spine setae interspersed with, or distal to, 8–10 smaller, narrower apical and subapical setae; endite with 4 marginal subapical setae on either side; surface of endite with 3 setae near midpoint. Maxilla 2 with endite entire. Maxilliped 1 with well developed exopodal flagellum bearing 3–4 terminal plumose setae; weakly bilobed epipod present; palp slender and lacking setae. Maxilliped 2 with well developed exopod extending to penultimate segment of endopod and bearing 2 terminal setae. Maxilliped 3 with ischio-merus incompletely fused, fused to basis; exopod well developed bearing 3–4 terminal plumose setae; exopod exclusive of setae extending nearly one-half length of endopod; arthrobranch absent.

Pereopod 1 not extending to distal end of antennal scale; fingers weakly bifid and approximately same length as palm; chela subequal to carpus in length; merus slightly longer than carpus. Pereopods 2 similar or occasionally dissimilar (one chela slightly more robust), both overreaching antennal scale by approximately length of fingers; fingers lacking teeth, having straight cutting edges, and equal in length to palm; carpus slightly shorter than chela, subequal to merus; ischium and merus equal in length. Pereopods 3–5 (Fig. 3c–f) nearly equal in size and shape, dactyls entire (not bifid), propodi with single spine on distal flexor margin. Pereopod 3 not extending to distal end of antennal scale; propodus 2.8 times length of dactyl and slightly more than twice length of carpus and ischium, with single distal spines on flexor margin; merus subequal in length to propodus. Pereopod 4 extending to distal end of second segment of antennular peduncle; propodus 2.8 times length of dactyl and slightly more than twice lengths of carpus and ischium; merus subequal in length to propodus. Pereopod 5 extending to proximal end of second segment of an-

Fig. 2. *Periclimenes patae,* new species. Mouth parts. a, mandible; b, maxilla 1; c, maxilla 2; d, maxilliped 1; e, maxilliped 3; f, maxilliped 2 (setation omitted). Scale equals 0.5 mm.

tennular peduncle; propodus and merus equal in length and 2.8 times length of dactyl; ischium 0.25 times longer than carpus; propodus with single row of comb setae on distolateral margin (Fig. 3f).

Uropodal exopods extending beyond telson for 0.2 times their length; strong movable spine between distolateral tooth and blade; movable spine distinctly longer than distolateral spine (Fig. 3h). Ovigerous females bearing 10–35 eggs. Eggs, depending on stage of development, range from 0.5 (undeveloped) to 0.7 mm (hatching stage) in maximum length.

Male.—Adults usually smaller (CL 2.2–3.2 mm), less robust, and with relatively larger pleopods than adult females. Rostrum relatively smaller than in female, not reaching beyond basal segment of antennular peduncle; typically armed with 4 dorsal teeth, less often with 5, and rarely 3 (Fig. 4a–d). More (15–20) clusters of antennular aesthetascs on large adult males than on large adult females. Appendix masculina (Fig. 3g) armed with 2–3 weakly serrate, apical and subapical spine-like setae; 3–5 simple spine-like setae along inner margin, distal-most usually subapical. Resemblance is similar to females in other respects.

Coloration.—The overall appearance of juveniles and adults in life is clear or transparent. The following description is of an adult ovigerous female. Pleopods clear. Pereopods clear except for a few patternless spots of aquamarine confined mainly to pereopods 2 and 5. Coxa and basis of all pereo-

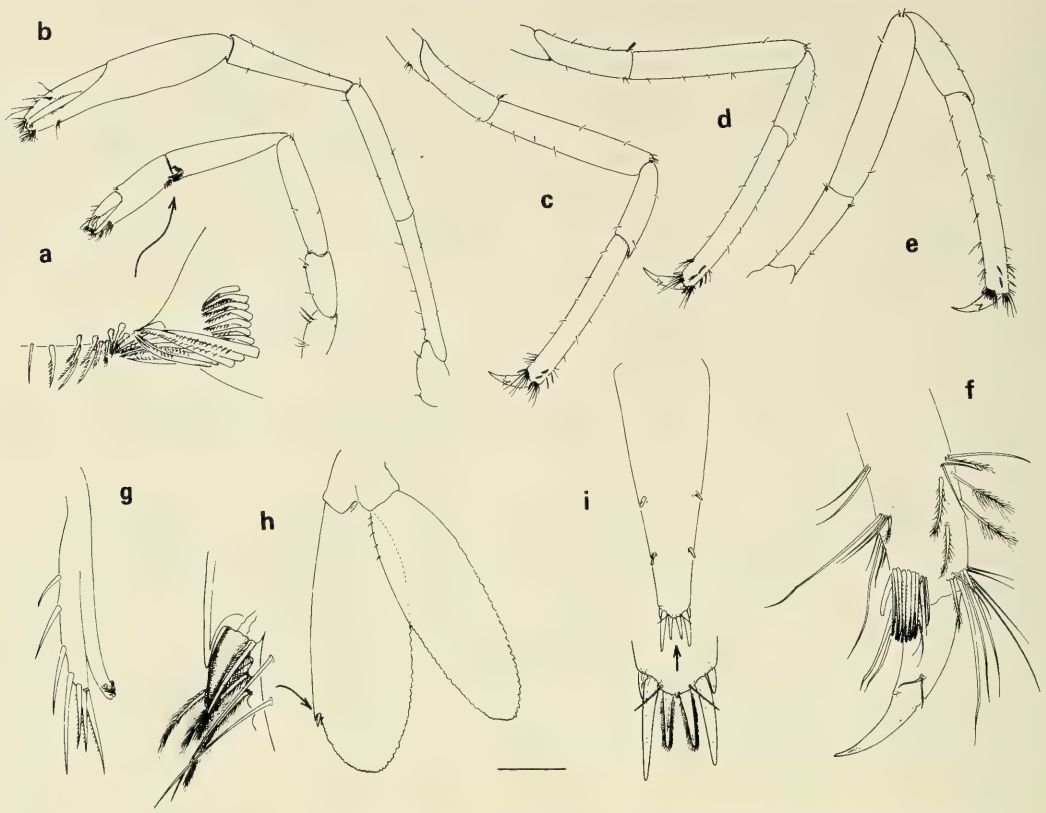


Fig. 3. *Periclimenes patae,* new species. a–e, pereopods 1–5; f, enlargement of dactyl and distal part of pereopod 5; g, appendix interna and appendix masculina from adult male; h, left uropod; i, telson. Scales equal 0.5 mm (a–e, h, i), and 0.1 mm (f, g).

pods with pale orange spots, coxa of pereopod 4 with a few spots of aquamarine. Cornea black with translucent golden covering, with dark reddish accessory pigment spot on proximal margin. Eyestalks with small, widely dispersed reddish orange spots mingled with fewer spots of pale orange. Suborbital area with squiggly aquamarine markings and intermingled spots of orange and aquamarine. Antennular peduncle traversed by two bands of pale orange, one slightly posterior to stylocerite, the other at posterior base of second antennular segment. Outer and inner antennular flagella and antennal scale with a few small russet spots. Antennular flagella and carapace clear. Antennal flagellum with light reddish orange bands.

Habitat.—Associated with the slimy sea plume (*Pseudopterogorgia americana*) and other gorgonians in depths of 1 to 12 m.

Distribution.—Off Pine Cay, Turks and Caicos Islands (British West Indies) and off Looe Key, Florida Keys, Florida.

Etymology.—The species is named for Patricia (Pat) Bubucis in recognition of her many contributions to our studies on the fauna of the Turks and Caicos Islands.

Remarks.—*Periclimenes patae* appears to be most closely related to *P. iridescens,* a species originally described by Lebour (1949) from a single adult female netted off Bermuda over water 180–200 m deep. Since its original description, *P. iridescens* has been reported from the western North Atlantic off Venezuela (Holthuis 1951), Tobago

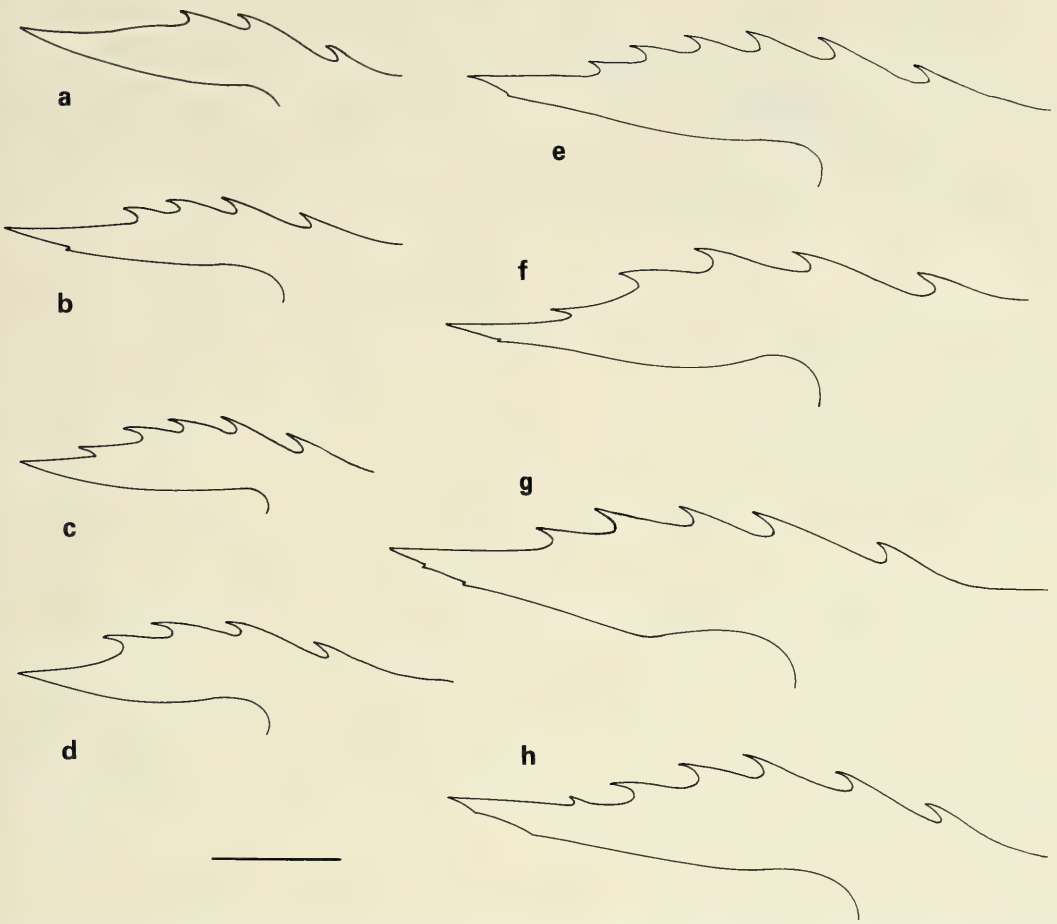


Fig. 4. *Periclimenes patae,* new species. Variation in the rostrums of adults. a–d, males; e–h, females. Scale equals 0.5 mm.

(Chace 1972), Curaçao (Criales 1980), Colombia (Criales 1984), Florida Gulf coast (Hopkins et al. 1977, Herbst et al. 1979, Williams 1984), and Cape Hatteras, North Carolina (Herbst et al. 1979, Williams 1984).

Periclimenes patae can be distinguished from the holotype of *P. iridescens* by having fewer rostral teeth (3–6), second pereopods equal or nearly equal in size and development, chelae of second pereopods lacking distinct tooth or teeth, dactyls entire (not bifid) on pereopods 3–5, and pereopods 3–5 each with single spine seta on the distoflexor margin of the propodus. Based on Lebour's (1949) description and our reexamination of the type specimen, *P. iridescens* (Fig. 5a–f) is characterized by: (1) seven dorsal teeth on rostrum (Fig. 5a, b), (2) distinctly unequal second pereopods, (3) a single rounded tooth on the dactyl of the major chela (Fig. 5d), (4) the dactyl of the major chela curving over and extending well beyond the fixed finger (Fig. 5d), (5) pereopods 3–5 having distinctly bifid dactyls (Fig. 5f), and (6) pereopods 3–5 each with 3 (Fig. 5f) or more sets of spine setae along distal third of propodal flexor margin. Additionally, Lebour's (1949) color notes suggest that *P. iridescens* is brightly "iridescent" in life. In contrast, *P. patae* is nearly transparent in life and does not appear iridescent.

The possibility of one or more unde-

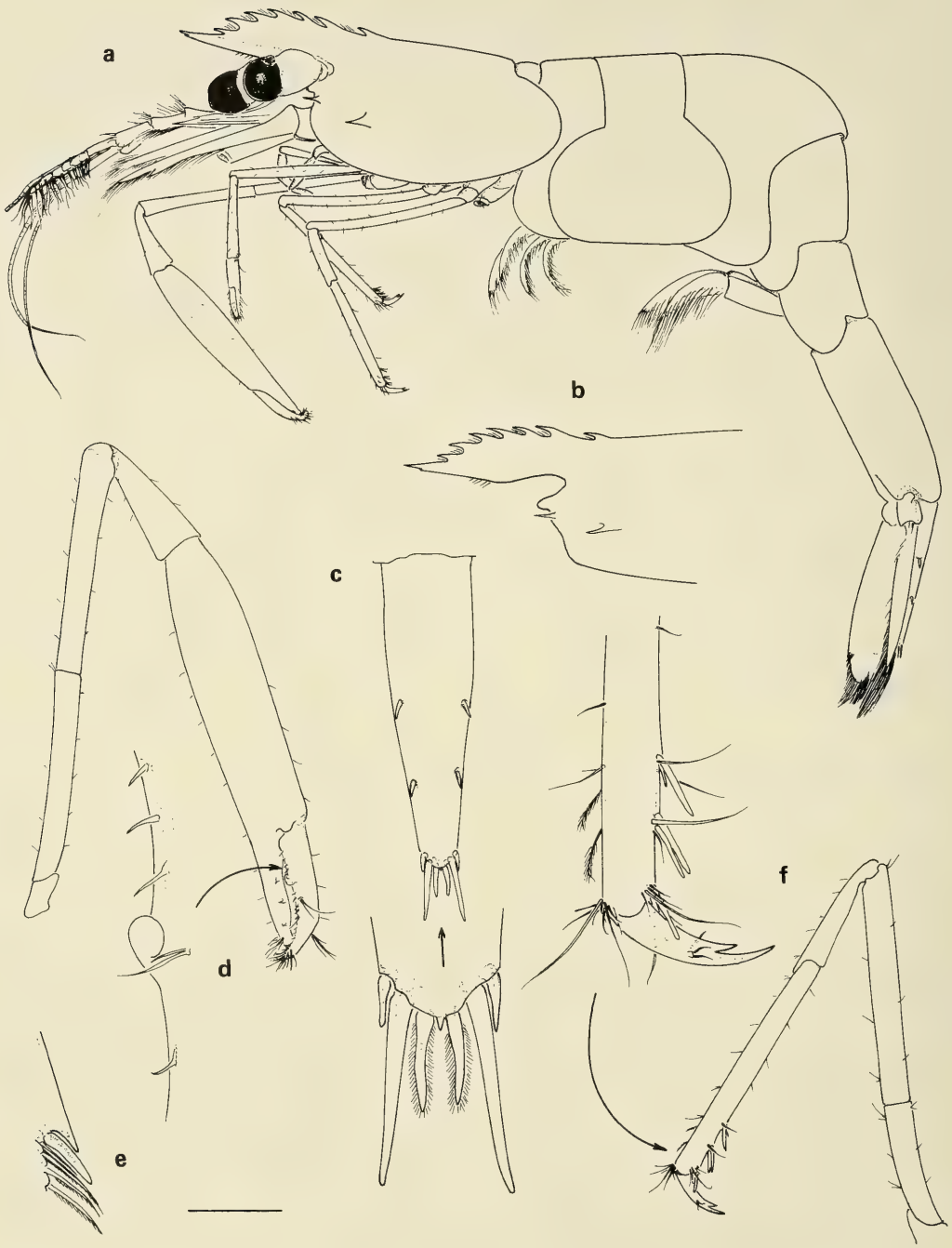


Fig. 5. *Periclimenes iridescens* (female holotype, BMNH). a, lateral view (right pereopods 3–5 and left pereopods 2 and 5 missing); b, lateral view of carapace; c, telson with enlargement of posterior tip; d, right pereopod 2 (major chela) with enlargement of tooth on dactyl; e, moveable spine on uropodal exopod; f, left pereopod 3, enlargement of dactyl and distal part of propodus. Scales equal 1.0 mm (a, b), 0.5 mm (c, d, f), and 0.2 mm (e).

scribed species within the "iridescens" complex was suggested by Herbst et al. (1979) and Criales (1980, 1984), who reported considerable variation in the specimens considered to be *P. iridescens.* Holthuis (1951) reported variation in the dactyls of the Venezuelan specimens that he assigned to *P. iridescens.* Some of his specimens had pereopods 3–5 with dactyls entire; others were transitional between entire and distinctly bifid. His material, like the holotype of *P. iridescens,* had distinctly dissimilar second pereopods, but the fingers of the major chelae, unlike those of the holotype, bore 2–3 teeth.

We examined the holotype of *P. iridescens,* the material examined by Holthuis (1951) and Herbst et al. (1979), and specimens from the Gulf of Mexico, Florida Keys, and deeper water off Pine Cay. In addition to *P. iridescens* and *P. patae,* we now believe that at least four closely related and undescribed species within the "iridescens" complex exist in the western North Atlantic. Descriptions of three of these new species are now in preparation.

Acknowledgments

Research was sponsored by the Oakleigh L. Thorne Foundation through a grant to Stephen Spotte. We thank Oakleigh B. Thorne, members and employees of the Meridian Club, and the Turks and Caicos government for support and encouragement. Patricia M. Bubucis, Roy R. Manstan, and Cherie S. Heard helped in the field and provided other technical assistance. Jerry A. McLelland inked the illustrations and aided in the field collections. Fenner A. Chace (USNM), Michael M. Dardeau (MESC), and Gabriele H. Meyer (GCRL) made constructive comments on the manuscript. J. P. Ellis of the British Museum (Natural History) kindly arranged the loan of the holotype of *P. iridescens.* We thank Brian Kensley, Raymond B. Manning, and Marilyn Schotte for the loan of material from the collections of the National Museum of Natural History. This is Contribution No. 76 of Sea Research Foundation, No. 226 of Marine Sciences Institute, and No. 1 of the Turks and Caicos Coral Reef Ecology Program.

Literature Cited

Chace, F. A., Jr. 1972. The shrimps of the Smithsonian-Bredin Caribbean Expeditions with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia).—Smithsonian Contributions to Zoology 98:1–179.

Criales, M. M. 1980. Commensal caridean shrimps of Octocorallia and Antipatharia in Curaçao and Bonaire with the description of a new species of *Neopontonides.*—Studies Fauna Curaçao 61:68–85.

———. 1984. Shrimps associated with coelenterates, echinoderms, and molluscs in the Santa Marta Region, Colombia.—Journal of Crustacean Biology 4:307–317.

Heard, R. W. 1986. Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) of the Northwest Atlantic. I. The genus *Neopontonides* Holthuis, 1951, with the description of *N. chacei,* new species, and the erection of *Pseudopontonides,* new genus, to receive *N. principis* Criales, 1980.—Journal of Crustacean Biology 6:471–484.

Herbst, G. N., A. B. Williams, & B. B. Boothe, Jr. 1979. Reassessment of northern geographic limits for decapod crustacean species in the Carolinian Province, USA; some major range extensions itemized.—Proceedings of the Biological Society of Washington 91:989–998.

Holthuis, L. B. 1951. A general revision of the Palaemonidae (Crustacea Decapoda Natantia) of the Americas. I. The subfamilies Euryrhynchinae and Pontoniinae.—Occasional Papers, Allan Hancock Foundation Publications 11:1–332.

Hopkins, T. S., D. R. Blizzard, S. A. Brawley, S. A. Earle, D. E. Grimm, D. K. Gilbert, P. G. Johnson, E. H. Livingston, C. H. Lutz, J. K. Shaw, & B. B. Shaw. 1977. A preliminary characterization of the biotic components of composite strip transects on the Florida Middle Grounds, northeastern Gulf of Mexico.—Proceedings of the 3rd International Coral Reef Symposium, Miami 1:37–47.

Lebour, M. V. 1949. Some new decapod Crustacea from Bermuda.—Proceedings of the Zoological Society of London 11(Part IV):1107–1117.

Williams, A. B. 1984. Shrimps, lobsters, and crabs

of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, pp. v–xvii, 1–550.

(RWH) Invertebrate Zoology Section, Gulf Coast Research Laboratory, P.O. Box 7000, Ocean Springs, Mississippi 39564-7000; (SS) Sea Research Foundation and Marine Sciences Institute, The University of Connecticut, Noank, Connecticut 06340.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 49–54

UPOGEBIA SPINISTIPULA, A NEW BURROWING SHRIMP FROM THE FLORIDA SHELF, NORTHEASTERN GULF OF MEXICO (DECAPODA: THALASSINIDEA: UPOGEBIIDAE)

Austin B. Williams and Richard W. Heard

Abstract.—*Upogebia spinistipula,* a new species of burrowing thalassinidean shrimp was taken in box core samples of live bottom material from a sector of the continental shelf in the northeastern Gulf of Mexico that lies off Panama City to Cape Romano, Florida. The rostrum of the small species (carapace length ca. 10 mm) resembles that of *U. lepta* from the tropical eastern Pacific, the tail fan resembles that of most species of *Upogebia* in the western hemisphere having an essentially rectangular telson, and the ventrally spined antennular and antennal peduncles resemble those of west Pacific species in the recently described genus *Gebiacantha.* The species apparently has no close relatives in the western Atlantic.

An undescribed species of *Upogebia* Leach, [1814] was discovered in box core samples taken on the continental shelf (carbonate platform, see Rezak et al. 1990) of the northeastern Gulf of Mexico. The collections were part of a Minerals Management Service (then Bureau of Land Management) sponsored baseline study referred to as the Mississippi-Alabama-Florida (MAFLA) Outer Continental Shelf Study (OCS) (see Phillips et al. 1990). Material used in the present investigation came from 11 of the 87 MAFLA stations distributed in 9 transects that were sampled for benthic infauna during 1975–1978. Stations where the new species was taken were scattered from southeast of Panama City, Florida, to west of Cape Romano in water depths ranging from 10 to 177 m (Fig. 1). All of the specimens are damaged, and many are fragmentary with legs usually detached or missing. The holotype and a series of paratypes have been deposited in the National Museum of Natural History (USNM). Paratypes to be transferred to the Museum of the Gulf Coast Research Laboratory (GCRL) are indicated.

Upogebia spinistipula, new species
Figs. 2–3

Material examined.—Sta. 2211, 27°56′29.5″N, 83°52′59.5″W, 43 m, coarse sand: USNM 239251, Holotype ♂, Nov 1977.—239252, Allotype ♀, Jul 1976.—Paratypes: 239260, 11 ♂, 7 ♀ (2 ovig.), 1 juv., Jul 1975 (4 ♂ and 2 ♀ ovig. to be transferred to GCRL).—239261, 2 ♂, 2 ♀ ovig., 2 other frags., Jul 1976.—239262, 1 ♀ ovig., Feb 1978.—239265, detached legs, 9 Aug 1977. Sta. 2528, 29°54′58.6″N, 86°04′58.5″W, 37 m, coarse sand: 239253, 3 ♀ ovig. & 1 probable ♂, Feb 1977.—1 ♂ cephalothorax, Sep 1977.—2 ♀ (1 ovig.), Feb 1978. Sta. 2531, 29°47′58.9″N, 86°09′28.9″W, 45 m, coarse sand: 239254, 3 ♀ (1 frag.), 7 Feb 1976.—1 juv., Nov 1977. Sta. 2532, 29°46′N, 86°12.5′W, 52 m, coarse sand: 239255, 1 tiny cephalothorax, Jul 1976. Sta. 2533, 29°42′59.9″N, 85°15′28.6″W, 67 m, coarse sand: 239256, 1 ♀ ovig., 26 Sep 1975.—1 tiny juv., 8 Feb 1976. Sta. 2534, 29°40′N, 86°17′W, 73 m, coarse sand: 239257, 1 ♂, Jul 1976. Sta. 2419, 29°46′59.8″N, 84°05′00.2″W, 10 m, medium fine sand:

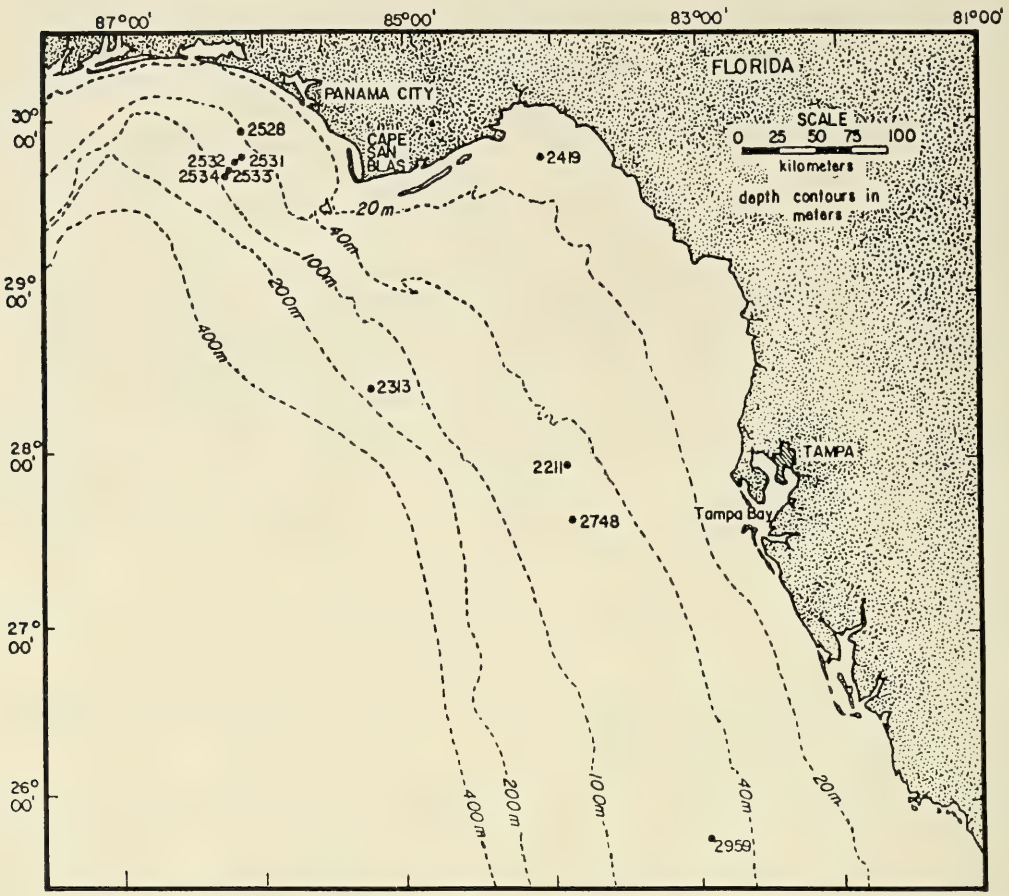


Fig. 1. BLM 77/88 MAFLA Survey station locations in northeastern Gulf of Mexico at which *Upogebia spinistipula,* new species, was collected. Station data are given in Materials Studied.

239258, 1 juv., Sep 1977. Sta. 2313, 28°23′59.3″N, 85°15′03.0″W, 177 m, clayey, sandy silt: 239259, 1 ♂, 20 Jan 1976. Sta. 2748, 27°37.2′N, 83°53.5′W, 50 m, coarse sand: 239263, 4 juvs. (2 frags.), Jul 1976.—1 ♂, 2 ♀, Nov 1977.—1 juv. frags., Feb 1978. Sta. 2959, 25°40′N, 83°05′W, 60 m, silty, very fine sand: 239264, 1 postlarva, 9 Aug 1977.

Diagnosis.—Rostrum bearing subapical pair of strong spines followed on each side by 5–7 strong spines. Projections to either side of elongate rostrum ending in acute spine. Postocular spine present. First and second abdominal segment lacking ventral spines; sixth segment lacking hooked anterolateral spine. Telson subrectangular. Antennular and antennal peduncles each bearing irregular row of ventral spines. Merus of cheliped lacking subdistal dorsal spine, carpus with 2–3 subequal spines on mesiodistal margin. Merus of leg 2 with proximal mesioventral spine, merus of leg 4 spineless.

Description.—Rostrum subtriangular, straight, narrow, tip exceeding eyestalks by distance at least ¾ their length; dorsal pair of strong, subapical spines followed on each lateral margin by 5–7 strong dorsal spines, ventral midline bearing 2–3 spines; dorsal surface bearing spiniform tubercles arranged more or less parallel to either lateral

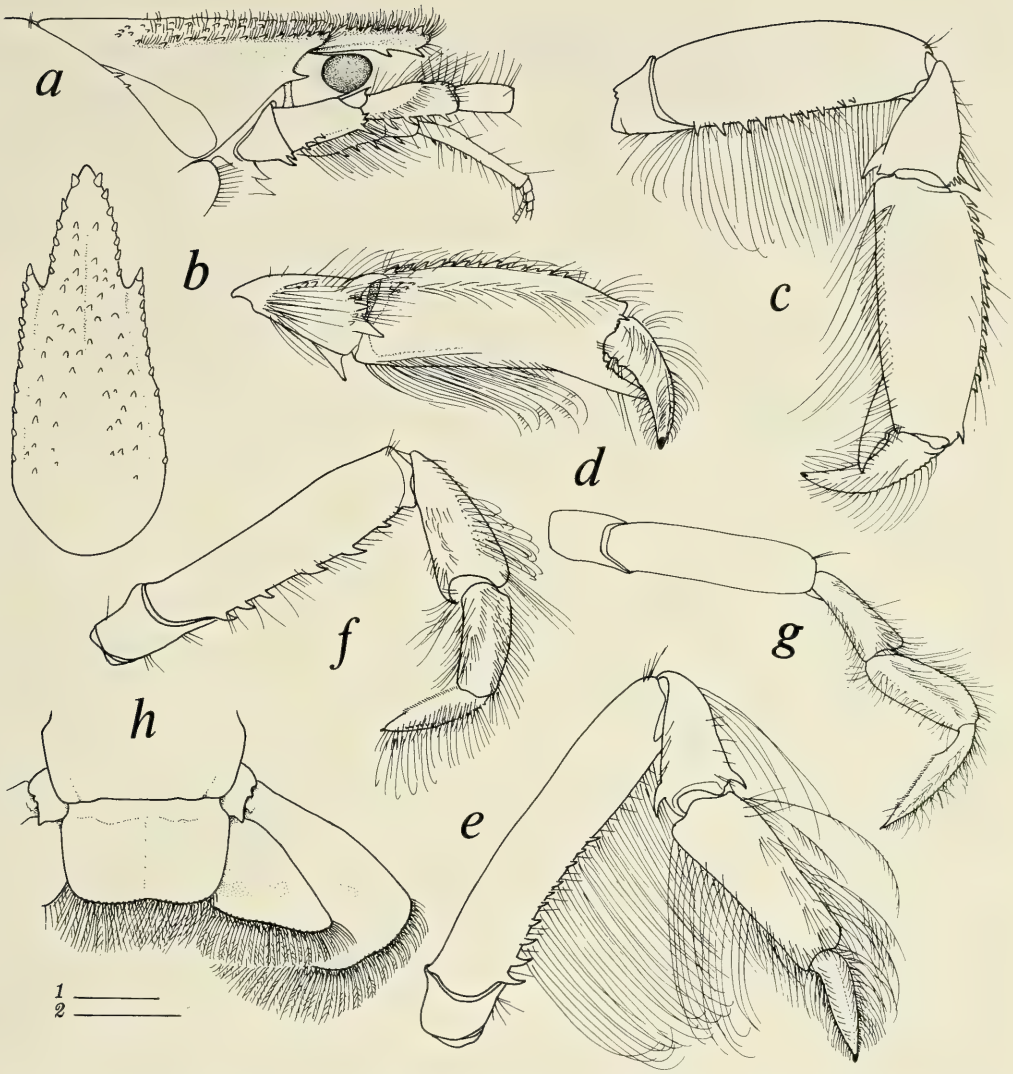


Fig. 2. *Upogebia spinistipula,* new species, ♂ Holotype: *a,* Cephalic region, lateral; *b,* Anterior carapace, dorsal; *c,* Right cheliped, lateral; *d,* Left chela and carpus, mesial; *e,* Leg 2; *f,* Leg 3; *g,* Leg 4; *h,* Telson and uropods. Scales = 1 mm: 1, *a, c, h*; 2, *b, d–g.*

margin and confluent with field of similar spines on anterior ⅔ of cephalic region, field angling toward sides posteriorly and diminishing to obsolescence; gastric surface posterior to this smooth; field of spines flanked on each side by posteriorly divergent furrow and that in turn by straight lateral ridge slightly diverging from median line posteriorly, each ridge bearing crest of about 8–10 spines, strongest on lateral rostral process and decreasing to obsolescence posteriorly. Shoulder flanking cervical groove bearing 1 or 2 spines below intersection with thalassinidean line; latter continued to posterior margin of carapace with slight interruption. Postocular spine present.

Abdominal sterna unarmed, terga glabrous, very few setae on margin of pleura 3–5.

Telson subrectangular, obsolescent trans-

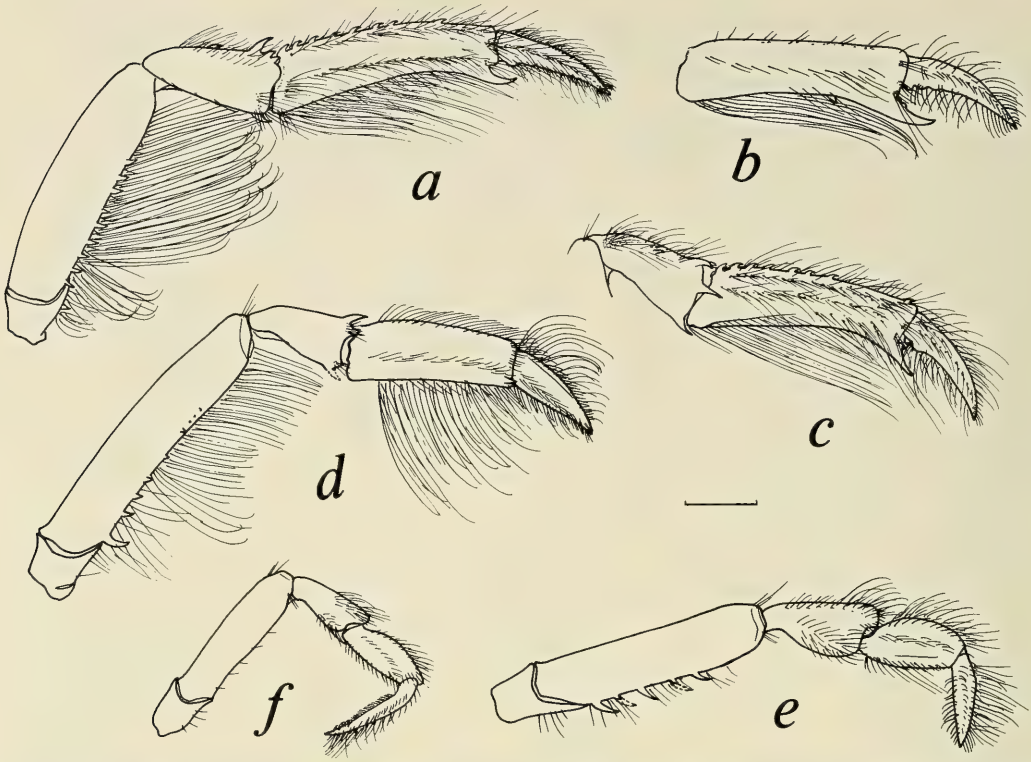


Fig. 3. *Upogebia spinistipula,* new species, ♀ Paratype: *a,* Right cheliped, lateral; *b,* Right chela rotated slightly to show ventral spine on palm; *c,* Left chela and carpus, mesial; *d,* Leg 2; *e,* Leg 3; *f,* Leg 4. Scale = 1 mm.

verse anterior ridge confluent with broader lateral ridge at each side, posterior margin with shallow concavity.

Eyestalk stout, eye as broad as distal diameter of stalk, directed anteriorly and laterally; stalk in lateral view concave dorsally, convex ventrally.

Antennular peduncle reaching slightly beyond terminal article of antennal peduncle, its proximal 2 articles together slightly shorter than terminal article; uneven row of spines on ventral margin of articles 1, 2 and proximal half of 3; flagella unequal, lower thinner ramus somewhat longer than thicker upper one.

Antennal peduncle with less than ⅓ its length (terminal article and distal part of penultimate article) extending beyond tip of rostrum, row of spines on ventrolateral margin of apparent articles 1 and proximal part of 2, ventromesial spines on article 2 continued as ventral row on article 3, terminal article spineless; scale moderate, triangular, tapered to acute terminal spine; flagellum, if extended, reaching beyond branchiostegite.

Maxilliped 3 without epipod.

Epistomial projection subquadrate in lateral view, bearing 2 strong spines on anterodorsal corner.

Chelipeds subequal. Coxa with slender anteriorly hooked spine on posteromesial margin. Ventral margin of ischium spineless. Merus lacking subdistal dorsal spine; row of 9–11 slender variably sized and arranged spines or tubercles on ventral margin. Carpus trigonal, shallow longitudinal groove laterally, lacking submarginal spine at anterior ventrolateral corner; mesiodorsal crest of 3 or more moderate to strong

spines behind prominent spine on anterior margin, 3 moderate spines on anterodorsal margin mesial to articulation with propodus; strong spine near middle of distomesial margin, and occasionally 1 or 2 smaller spines on margin above it, ♂ sometimes with tubercles on proximomesial surface near anteromesial spines. Palm suboval in cross section, length including fixed finger about 2.4 times height near midlength in ♂, 5.5 times height in ♀; bearing longitudinal rows of mixed plumose and long setae on all surfaces, longest ventrally; palm of ♂ with obsolescent dorsal ridge, paralleling this a mesiodorsal row of forwardly bent or hooked spines, and on proximomesial margin beneath overhanging prominent anterodorsal spine of carpus a slightly sigmoid row of spiniform tubercles; distomarginal spine below mesial dactylar condyle, 1–3 smaller spines ventral to this on distal margin of palm; lower mesial surface usually spineless, but often in ♂ and occasionally in ♀ a spine on ventral margin of palm about ⅔ distance from proximal margin; low ridge running obliquely anteriad from heel of palm to become obsolescent at midlength. Fixed finger short, slender, downcurved from palm and tapering anteriorly to slender tip, 2–5 obsolescent teeth on proximal prehensile edge. Dactyl stouter than fixed finger and far overreaching it, setose, toothless, tip corneous.

Legs 2–5 elongate and slender. Leg 2 reaching about to distal ¼ of cheliped palm; carpus with slender, acute distodorsal spine and similar but smaller subdistal ventral spine; merus without subdistal dorsal spine, proximal mesioventral spine succeeded distally by 5–7 ventral spines diminishing in size along row; coxa with strong proximomesial spine. Leg 3 with merus bearing ventral row of 5–9 spines; ischium unarmed; coxa of ♀ with flange-like low spine lateral to gonopore. Leg 4 with merus and ischium unarmed, dactyl longer than propodus. Subchelate leg 5 reaching beyond ischium of cheliped.

Uropod with ovate exopod far overreaching subtriangular endopod, tiny acute spine on protopod above base of endopod.

Measurements in mm.—Holotype ♂: length anterior carapace 6.8, length carapace 10.9, length chela including fixed finger 7.7, height palm near midlength 2.8; allotype ♀, same measurements: 4.0, 6.8, 2.8, 0.77.

Known range.—Confined to the material examined (see Fig. 1).

Etymology.—From the Latin "spina," spine, and "stipula," stalk, for the spined antennular and antennal peduncles. It is a noun in apposition.

Remarks.—*Upogebia spinistipula,* new species, has an unmodified tail fan with essentially rectangular telson, being morphologically similar in this respect to the majority of upogebiid species in the western hemisphere. In other respects, however, the species differs from western Atlantic congeners. The ventrally spiny antennular and antennal peduncles, for which the species is named, are shared by no other known representatives in the region, but these articles are so spined in some species of the newly erected *Gebiacantha* Ngoc-Ho, 1989, which contains several representatives from the Indo-West Pacific region. *Gebiacantha acutispina* (de Saint Laurent & Ngoc-Ho, 1979) and *G. reunionensis* Ngoc-Ho, 1989 are perhaps closest to *U. spinistipula* with respect to these structures. *U. spinistipula* has one postorbital spine, but species of *Gebiacantha* have two or more postorbital spines. The relatively smooth but sexually dimorphic chelipeds of *U. spinistipula* are devoid of strong ventral spines characteristic of *Gebiacantha* species.

The long slender rostrum of *U. spinistipula* bears some resemblance to that of *U. lepta* Williams, 1986, from the eastern Pacific. The dorsal surface of the rostrum of the former bears small spines in addition to those along the rostral margin, whereas in *U. lepta* the dorsal surface, except for the margin, is spineless. *U. spinistipula* there-

fore seems to stand apart in a number of respects from other species in the family.

Acknowledgments

The manuscript benefitted from the constructive comments of Bruce B. Collette, Brian Kensley, Raymond B. Manning, and an anonymous reviewer. We are grateful to Hans G. Kuck for sorting the material and preliminary work on identification, and to Keiko Hiratsuka Moore for preparing the illustrations. Specimens studied were collected under Bureau of Land Management contracts to the State University System of Florida Institute of Oceanography (contract 08550-CT-11) and to Dames and Moore (contract AA550-CT7-34).

Literature Cited

De Saint Laurent, M., & N. Ngoc-Ho. 1979. Description de deux espèces nouvelles du genre *Upogebia* Leach, 1814 (Decapoda, Upogebiidae).—Crustaceana 37(1):57–70.

Leach, W. E. [1814]. Crustaceology. *In* Edinburgh encyclopaedia 76:383–437, pl. 221, Edinburgh [Scotland].

Ngoc-Ho, N. 1989. Sur le genre *Gebiacantha* gen. nov., avec la description de cinq espèces nouvelles (Crustacea, Thalassinidea, Upogebiidae).—Bulletin du Muséum National d'Histoire Naturelle, Serie 4, Section A 11(1):117–145.

Phillips, N. W., D. A. Gettleson, & K. D. Spring. 1990. Benthic biological studies of the southwest Florida shelf.—American Zoologist 30(1):65–75.

Rezak, R., S. R. Gittings, & T. J. Bright. 1990. Biotic assemblages and ecological controls on reefs and banks of the northwest Gulf of Mexico.—American Zoologist 30(1):23–35.

Williams, A. B. 1986. Mud shrimps, *Upogebia*, from the eastern Pacific (Thalassinoidea: Upogebiidae).—San Diego Society of Natural History, Memoir 14:1–60.

(ABW) National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, D.C. 20560; (RWH) Gulf Coast Research Laboratory, P.O. Box 7000, Ocean Springs, Mississippi 39564-7000.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 55–63

A NEW TROGLOBITIC CRAYFISH, *PROCAMBARUS* (*LONNBERGIUS*) *MORRISI*, (DECAPODA: CAMBARIDAE) FROM FLORIDA

Horton H. Hobbs, Jr. and Richard Franz

Abstract.—*Procambarus* (*Lonnbergius*) *morrisi,* an albinistic troglobite, is described from Devil's Sink, seven kilometers west of Interlachen, Putnam County, Florida. Having its closest affinities with *P.* (*L.*) *acherontis* (Lönnberg), it is the second crayfish to be assigned to the subgenus. It may be distinguished from the latter species by possessing a well developed cephalic process on the first pleopods of first form males and by the looped sculpturing on the annulus ventralis in the females. This is the only albinistic crayfish in which the first pleopod of the male lacks a mesial process. Emended diagnoses of the subgenus and *P.* (*L.*) *acherontis* are presented.

The discovery of *Procambarus* (*Lonnbergius*) *morrisi* in Devil's Sink, Putnam County, Florida, extends the northeastern limit of the geographic range of the troglobitic crayfishes of Florida to the southern flank of Trail Ridge. There the latter forms the drainage divide between the St. Johns River, which flows into the Atlantic Ocean, and the Santa Fe River, a major tributary of the Suwannee River that flows into the Gulf of Mexico. Surprisingly the closest relative of this crayfish is not one of the troglobites, the ranges of which are most proximate (less than 40 km to the southwest and west) and encompass parts of the Santa Fe Basin. Rather, it is another albinistic form, *P.* (*L.*) *acherontis* (Lönnberg, 1894), which inhabits subterranean waters in the area of headwaters of the St. Johns River, some 120 km to the south.

These crayfishes are obviously closely allied, and the differences noted between them are largely limited to those occurring in the secondary sexual features. Inasmuch as the diagnosis of the previously monotypic subgenus *Lonnbergius* (Hobbs, 1972) was identical to that of *P.* (*L.*) *acherontis,* there is need to modify it to include the new species. Moreover, specimens of *P.* (*L.*) *acherontis* from additional localities necessitate at least a slight modification of the diagnosis of that species. These diagnoses precede the diagnosis and description of *P.* (*L.*) *morrisi.*

Subgenus *Lonnbergius*

Diagnosis.—(Modified from Hobbs 1972: 8.) Albinistic; eyes reduced and without pigment. Rostrum with pair or several marginal spines or tubercles but lacking dorsomedian longitudinal carina. Carapace without cervical spines. Areola 7.3 to 23.8 times as long as broad and constituting 38.1 to 45.6% of entire length of carapace (45.7 to 54.7% of postorbital carapace length). First three pairs of pereiopods without conspicuous brush of setae extending from basis to merus. Hooks on ischia of third and fourth pereiopods simple or bituberculate. Coxa of fourth pereiopod with prominent vertically disposed caudomesial boss. First pleopod reaching coxa of third pereiopod, symmetrical, with proximomedian lobe but lacking proximomesial spur; no shoulder on cephalic surface; subapical setae present or absent. Terminal elements of first pleopod in first form male consisting of mesial process which present or absent; cephalic pro-

cess well developed, rudimentary, or absent; prominent caudal process, flanked by protuberances on ridge of caudal knob; and very conspicuous, subacute, distally directed central projection. (Mesial lamella much shorter than in other members of genus, exposing much of median lamella proximal to bases of caudal element and centrocaudal process.) Mesial ramus of uropod with median spine acute but never reaching distal margin of ramus. Female with caudally projecting tuberculate, often spiniform, prominences lateral to median cleft on tuberculate sternite immediately cephalic to annulus ventralis.

Remarks.—The discovery of the new crayfish described herein necessitates a modification of couplet 14 in Hobbs' (1972: 4) key to the subgenera of the genus *Procambarus* as follows:

14(13′)	Bituberculate hooks on ischia of third and fourth pereiopods (fig. 1*i*) or mesial process of first pleopod absent	*Lonnbergius*
14′	Bituberculate hooks never present on ischia of both third and fourth pereiopods (fig. 1*i*); mesial process of first pleopod always present	15

Procambarus (*Lonnbergius*) *acherontis* (Lönnberg, 1894)

Cambarus acherontis Lönnberg, 1894:125.
Procambarus acherontis.—Hobbs, 1942: 342.

Diagnosis.—Areola 14 to 23.8 times as long as broad, comprising 41 to 44% of entire length of carapace, 49.8 to 52.6% of postorbital carapace length. Ischium of third and fourth pereiopods with bituberculate hooks. First pleopod of first form male with or without subterminal setae, if present, limited to longitudinal row of 3 to 5 sparsely plumose setae on cephalic margin; slender mesial process of variable length, ranging from falling short of to almost reaching distal margin of shaft of appendage; cephalic process rudimentary or absent; caudal element consisting of small, corneous, cephalodistally directed caudal process flanked by bulges on distal rim of caudal knob; and corneous, compressed, subtriangular, distally directed central projection situated anterior to and slightly overreaching caudal process; rudimentary process lacking from distal rim of lateral lamella between cephalic and caudal processes. Female with annulus ventralis bearing cephalolateral tubercles and caudomedian sinuous sinus.

Procambarus (*Lonnbergius*) *morrisi,* new species
Fig. 1

Cavernicolous crayfish from Putnam County [Florida].—Franz & Franz 1991.

Diagnosis.—Areola 7.3 to 12.7 times as long as broad, constituting 38.6 to 45.6% of entire length of carapace, 47.1 to 51.8% of postorbital carapace length. Ischium of third and fourth pereiopods never with clearly defined bituberculate hooks. First pleopod of first form male with row of 2 or 3 subterminal plumose setae at caudomesial base of cephalic process; mesial process absent; cephalodistally directed cephalic process well developed, acute, subtriangular, and almost reaching or slightly overreaching apices of other terminal elements; caudal element consisting of small, corneous cephalodistally directed caudal process arising from rim of caudal knob; compressed, corneous central projection extending distally between caudal and cephalic processes; and short, rounded, rudimentary process borne on distal rim of lateral lamella between cephalic and caudal processes. Female with subtriangular annulus ventralis, lacking cephalolateral tubercles but bearing caudoventral complexly looped sinus.

Holotypic male, form I.—Body subovate, distinctly depressed (Fig. 1a, l). Abdomen narrower than thorax (8.5 and 11.1 mm). Greatest width of carapace at about 0.2

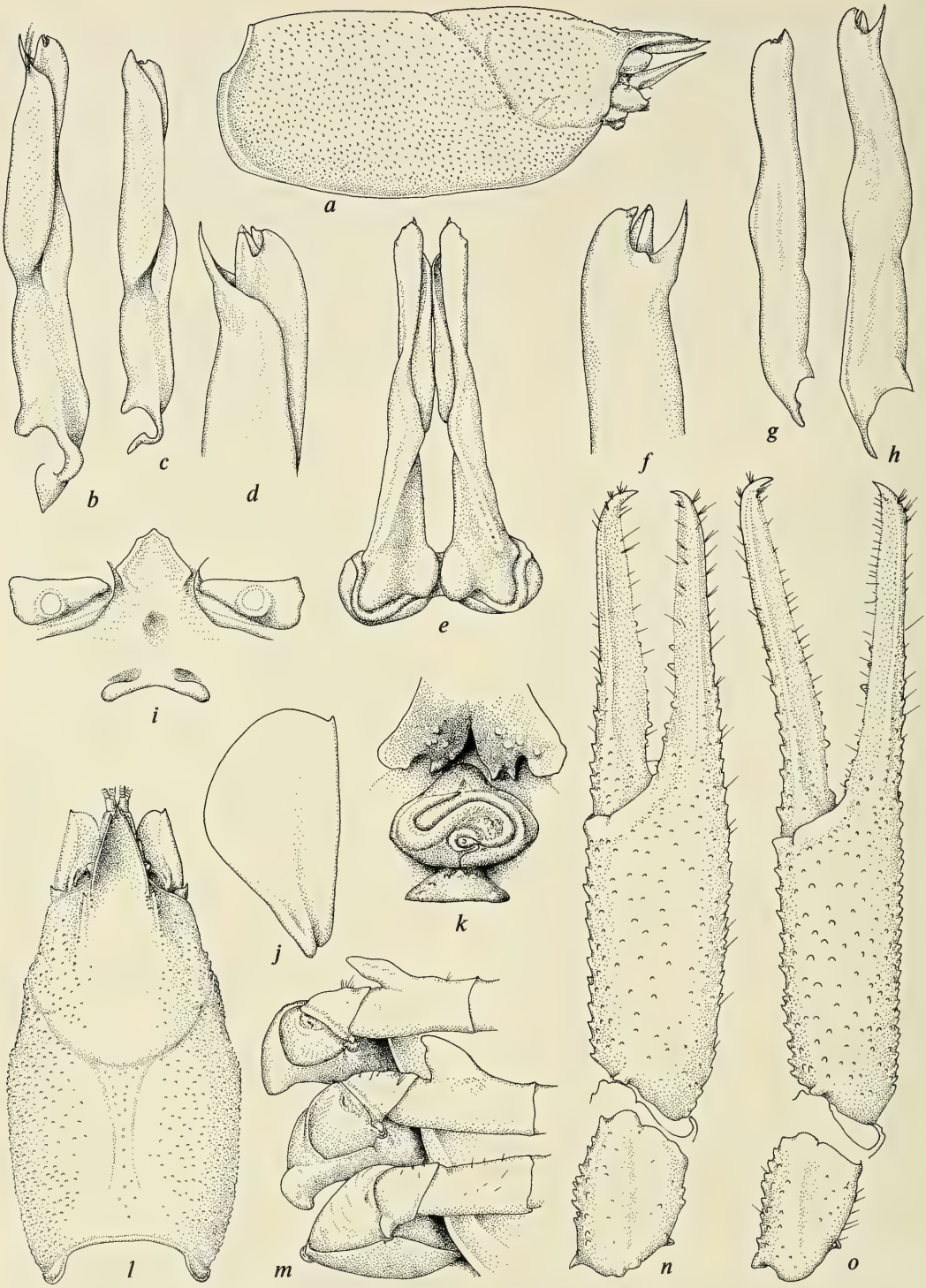
length of areola from cephalic margin where width greater than height (11.1 and 8.1 mm); width noticeably constricted at level of caudodorsal margin of cervical groove. Areola 8.1 times as long as broad, comprising 38.6% of entire length of carapace (47.1% of postorbital carapace length) and, although with room for more, bearing single sublinear series of punctations in narrowest part. Cephalic section of carapace 1.6 times as long as areola. Surface of carapace punctate over rostrum, dorsal gastric region, areola, and orbital and antennal regions; otherwise mostly tuberculate. Rostrum comparatively broad basally, tapering to marginal spines at base of short acumen, latter reaching midlength of ultimate podomere of antennular peduncle; rostral margins slightly thickened and finely subserrate posteriorly and anteriorly, less distinctly so between margins; dorsal surface concave, lacking median carina. Subrostral ridges weak and evident in dorsal aspect only along basal fifth of rostrum. Postorbital ridges well defined, marked by linear series of tubercles posteriorly and terminating in short, acute, corneous tips. Suborbital angle represented by low rounded bulge. Branchiostegal spine virtually wanting; caudal flank of cervical groove with row of small tubercles, of which one probably homologous to cervical spine but not recognizable as such.

Abdomen subequal in length to carapace. Pleura of third through sixth segments truncate ventrally; those and that of second segment with caudoventral extremity angulate. Cephalic section of telson with 1 (right) or 2 (left) fixed spines in caudolateral corners. Cephalic lobe of epistome (Fig. 1i) subpentagonal in outline, with elevated (ventrally) margins; main body with prominent anteromedian depression containing anteriorly situated fovea. Ventral surface of proximal podomere of antennular peduncle with prominent spine at about midlength. Antennal peduncle with moderate spine on both basis and ischium; flagellum (about 60 mm in length) overreaching abdomen by about 10 mm. Antennal scale (Fig. 1j) 1.8 times as long as wide, broadest slightly distal to midlength; greatest width of lamellar area almost twice that of thickened lateral part.

Third maxilliped reaching base of ultimate podomere of antennular peduncle; ischium not produced distolaterally, bearing short, simple setae, but longer ones on postaxial flank of crista dentata and at mesial base.

Right chela (Fig. 1o) subovate in cross section, weakly depressed; length of mesial margin of palm about 2.2 times width, little more than 0.33 total length of chela; entire palm studded with tubercles, although irregularly arranged along mesial margin of palm, 12 to 14 appearing in silhouette. Both fingers with well defined dorsal and ventral longitudinal ridges flanked by tubercles proximally and setiferous punctations more distally. Opposable margin of fixed finger with row of 5 dorsally situated tubercles in proximal third, followed by row of 3 (proximalmost largest on margin) more ventrally situated ones in adjacent seventh; very narrow band of minute denticles beginning almost at base of finger, and broadening at level of largest tubercle, continuing distally to base of distal tenth of finger before tapering to base of corneous tip; lateral surface of finger with tubercles along proximal half and row of setiferous punctations distally. Opposable margin of dactyl with row of about 10 tubercles (second from base largest, and more distal ones no larger than, and difficult to distinguish from, adjacent minute denticles) extending from base slightly beyond midlength of finger; minute denticles distributed as on fixed finger; mesial surface with tubercles scattered basally, but cluster narrowing distally with single distalmost tubercle situated just proximal to midlength of finger.

Carpus of cheliped longer than broad with shallow median longitudinal depression flanked mesially by sublinear series of tubercles and laterally by few smaller tubercles and punctations; mesial surface tuber-


a
b
c
d
e
f
g
h
i
j
k
l
m
n
o

culate, but no tubercle conspicuously more prominent than others; ventral and lateral surfaces more sparsely tuberculate, ventrodistal margin with large tuberculiform condyle and more mesial single tubercle larger than others proximal and lateral to it.

Merus entirely tuberculate although weakly so proximomesially and proximolaterally; almost all of dorsal margin serrate with no tubercles conspicuously larger than others nearby; ventral surface with irregular mesial row of 17 or 18 tubercles extending almost from base to distal end of podomere and poorly defined lateral row of 16 or 17; other tubercles present to the sides of both rows. Tuberculate ischium with mesial row of 7 tubercles; suflamen well developed.

Hooks on ischia of third and fourth pereiopods (Fig. 1m), that on third more slender, reaching much proximal to basioischial articulation, and opposed by conspicuous tuft of setae, but no tubercle, on basis; hook on fourth pereiopod robust with undulating proximal margin suggesting bituberculate condition of hooks in *P.* (*L.*) *acherontis.* Coxa of fourth pereiopod with strong vertically disposed caudomesial boss; that of fifth pereiopod with tuberculiform boss.

Sternum between third, fourth, and fifth pereiopods moderately deep; ventrolateral margins with such delicate plumose setae that although covered ventrally, pleopods in usual position clearly visible.

First pleopods (Fig. 1b, d, e, f, h) as described in "Diagnosis."

Uropods with lobes of basal podomere bearing acute spines; both rami broad and with distolateral spine; distomedian spine of mesial ramus situated much proximal to broadly rounded distal margin.

Table 1.—Measurements (mm) of *Procambarus* (*Lonnbergius*) *morrisi,* new species.

	Holotype	Allotype	Morphotype
Carapace			
Entire length	21.0	18.8	17.9
Postorbital length	17.2	15.8	14.2
Width	11.1	10.8	9.4
Height	8.1	7.9	7.2
Areola			
Width	1.0	0.7	0.8
Length	8.1	7.5	7.0
Rostrum			
Width	3.0	2.8	2.2
Length	4.0	3.5	3.3
Right chela			
Length, palm mesial margin	6.7	5.0	5.4
Palm width	3.0	2.9	2.5
Length, lateral margin	17.2	12.6	15.0
Dactyl length	9.5	6.2	7.0
Abdomen			
Width	8.5	7.9	6.8
Length	21.0	18.3	17.8

Allotypic female.—Differing from holotype, other than in secondary sexual features in following respects (See Table 1 for differences in proportions of carapace and chela.): areola 10.7 times as long as wide; rostrum reaching base of ultimate podomere of antennular peduncle; branchiostegal spine very small and acute; telson with 2 fixed spines in each caudolateral corner; third maxillipeds not quite reaching distal end of proximal podomere of antennular peduncle, distolateral angle produced in short,

←

Fig. 1. *Procambarus* (*Lonnbergius*) *morrisi,* new species (holotype except c, g from morphotype, and k, n from allotype): a, lateral view of carapace; b, c, mesial view of first pleopod; d, distal part of first pleopod in mesial view; e, caudal view of first pleopods; f, distal part of first pleopod in lateral view; g, h, lateral view of first pleopod; i, epistome and part of basal podomeres of antennae; j, antennal scale; k, annulus ventralis and adjacent sternites; l, dorsal view of carapace; m, basal podomeres of third, fourth, and fifth pereiopods; n, o, dorsal view of distal podomeres of cheliped.

acute spine. Opposable margin of fixed finger of chela (Fig. 1n) with dorsally situated row of 3 tubercles and more ventral one of 2, opposable margin of dactyl with row of 7 tubercles, minute denticles on both fingers arranged in single row; merus with ventrolateral row of 21 tubercles and ventromesial one of 18; ischium with row of 6 tubercles mesially.

Annulus ventralis (Fig. 1k) subtriangular in ventral aspect with complexly contoured, oval, ventral face. Sinus originating on cephalomedian margin of latter and, after extending caudodextrally to near dextral margin, making hairpin turn and coursing in broad arc to near sinistral margin, there looping dextrally and slightly cephalically to median line where turning caudally and describing almost complete circular course before turning caudodextrally to median line and finally caudally to caudal margin of annulus.

Sternum immediately cephalic to annulus broadly V-shaped, deeply cleft, tuberculate, with two pairs of conspicuous, acute, caudally projecting prominences flanking and partly overhanging (ventrally) cephalic part of annulus. Postannular sclerite also subtriangular, three-fourths as wide as annulus, and bearing arc of tubercles. First pleopods uniramous but well developed.

Morphotypic male, form II.—Differing from holotype in following respects (See Table 1 for differences in proportions of carapace and chela.): tiny speck of brown pigment in right eye; apex of rostrum reaching base of ultimate podomere of antennular peduncle; branchiostegal spine well developed; cephalic section of telson with two pairs of spines in caudolateral corners; cephalic lobe of epistome subtrapezoidal with single prominent tubercle; antennal flagellum (about 57 mm in length) overreaching telson by approximately one-third of its length; third maxilliped reaching midlength of penultimate podomere of antennular peduncle, ischium produced distolaterally in small spine. Opposable margin of fixed finger of chela with dorsally situated row of 4 tubercles and more ventral one of 5; opposable margin of dactyl with row of 7 tubercles; minute denticles on both fingers mostly arranged in single row as in allotype; merus of cheliped with ventromesial row of 21 tubercles and ventrolateral one of 16; hooks on ischia of third and fourth pereiopods reduced to knobs, neither overreaching basioischial articulation; boss on caudomesial angle of coxa of fourth pereiopod prominent but less well defined.

First pleopod (Fig. 1c, g) with hoodlike, acute cephalic process largest of terminal elements, none of which corneous, and overreaching others; caudal process not differentiated from caudal knob; central projection tuberculiform, not reaching so far distally as caudal element; rudimentary process on distolateral margin of lateral lamella so reduced as to appear no more than slight bulge.

Type locality.—Devil's Sink, 152 m north of St. Rte. 20, 7.1 km west of Interlachen (junction of St. Rtes. 313 and 20), Putnam County, Florida (NE ¼, SE ¼, NW ¼, Sec. 13, Twp. 10S, R. 23E). Devil's Sink is located near the summit of a prominent sand ridge (elevation 45.7 m), approximately 220 m north of the northwest edge of Lake Galilee. The nearly circular rim of this steep-sided sink is approximately 30.5 m in diameter. The eastern and southern sides have been severely eroded by foot traffic, while the other slopes are forested with *Liquidambar styraciflua* and members of the genus *Quercus*. Five meters above the pool the diameter of the sink narrows to less than 18 m and continues to a vertical, water-filled shaft of similar dimension. The shaft reaches a maximum water depth of 31.7 m. A large detritus cone of sediment (surface debris and a Volkswagen car!) rises from the base of the sink to a water depth of 16.8 m. A small passage, approximately 30.5 m in length and leading southwest from the shaft, slopes to a small terminal room 3.7 by 6.1 m and 6.0 to 3.1 m in height. Maximum

water depth there is 37.5 m. Water in the cave is stratified, with the bottom layer having a rusty color and a slightly cooler temperature (22°C) than the clear upper layer. The limestone in contact with the rusty-water zone is stained, resembling a stained bath tub. The ceiling of the terminal room has dark areas with growths of possible iron bacteria and hanging strands of what may be sulfur bacteria. Crayfish were found only in the sloping passage and terminal room; none was observed in the shaft. They were found both in the rusty and clear water zones and appeared to move freely from one to the other. The exoskeletons of many of the individuals observed were stained with the color of the rusty water. Specimens of unidentified troglobitic amphipods were found with the crayfish in the cave. Centrarchid fishes were observed in the upper portions of the water column in the shaft, but not in the sloping passage and terminal room.

Geological notes.—Sediments that outcrop in the upper portions of the sink consist of coarse variegated sands associated with the Cypress Head Formation (=Citronelle Formation of Cooke 1945:236). Phosphatic clays of the Hawthorn Formation are exposed about 4.6 m above the sinkhole pool. The shaft is developed in this unit to a water depth of 31.7 m, at which level the Crystal River Formation is encountered. The small passage and terminal room are situated in the latter formation.

Disposition of types.—The holotype, allotype, and morphotype (♂ I, ♀, ♂ II) are deposited in the National Museum of Natural History (Smithsonian Institution) nos. 220374, 220375, and 220376, respectively, as are the paratypes, consisting of 2 ♂ I, 6 ♀, and 4 juvenile ♂.

Size.—The largest specimen available is the holotype which has a carapace length of 21.0 mm (postorbital carapace length 17.2 mm). The smallest first form male has corresponding lengths of 20.0 and 16.3 mm. Ovigerous females or ones carrying young have not been collected.

Range and specimens examined.—This crayfish is known only from the type locality. Two collections have been made by Tom Morris, one on 9 May 1989 consisting of 3 ♀ and 4 juv. ♂; the second one, with the assistance of Paul Smith, from minnow traps set at 33.5 m water depth on 6 March 1990 and retrieved two days later, consisting of 3 ♂ I, 1 ♂ II, and 4 ♀.

Devil's Sink is located in the extensive sand hill district associated with the Interlachen Karstic Highland (Pirkle & Pirkle 1984) on the southern flank of Trail Ridge. Dissolution of underlying carbonates of the Hawthorn Formation (Miocene) and the Ocala Limestones (Eocene) have secondarily modified the landscapes, particularly in the inter-dune areas, to form circular depressions. Many of these sinks are filled with water and form lakes and ponds in the region. Paleo-sinks that open in some of the lake basins are usually filled with sediments and do not openly connect with underlying carbonate rocks. Deevey (1988) has calculated leakage rates through these sinks for several of the lakes in this area. To our knowledge, Devil's Sink is the only such sinkhole in the entire area that has a direct connection with a carbonate aquifer in the entire southern Trail Ridge region. The surficial aquifer that controls lake levels in the area has a water quality different from that found in Devil's Sink.

Variations.—In addition to the variations pointed out in the primary types, the rostral margins may be clearly serrate or subtly so, and the number of tubercles at the base is usually fewer than in the holotype. The anterior lobe of the epistome is more frequently subrhomboidal than pentagonal and the tubercle noted in the allotype is unique among our specimens. The cephalic section of the telson may bear one to three spines in the caudolateral corner. Details of the hooks on the ischia of the third and fourth pereiopods are decidedly variable, and in one of the first form males the distal extremity of the hooks is concave, suggesting

the clearly bituberculate condition of the hooks on *P.* (*L.*) *acherontis.* The sternum immediately anterior to the annulus ventralis in all of the females is tuberculate, and there are always projections extending posteriorly from the margin, a large pair flanking the median cleft and occasionally smaller ones that, like the large ones, may be spiniform or rounded.

Relationships.—As stated in the introductory remarks, *Procambarus* (*Lonnbergius*) *morrisi* has its closest affinities with *P.* (*L.*) *acherontis.* Disregarding the secondary sexual features, with the exception of the narrower areola of *morrisi,* one would have difficulty in recognizing this crayfish as different from Lönnberg's species. Similarities are also readily evident in the structure of the first pleopod of the male, especially that of first form individuals: the long, only slightly reflexed shaft, the comparatively short mesial lamella, the arrangement of the caudal process and caudal knob, and the distally directed central projection. Pertinent also is their unique sharing of the entocytherid symbiont cited under "Associates."

Several features in addition to the short areola (less than 11 times as broad as long) serve to distinguish *morrisi* from *acherontis*: the hooks on ischiopodites of the third and fourth pereiopods are not bituberculate; the cephalic process of the first pleopod is well developed; the mesial process is lacking; and no cephalolateral tubercles are present on the annulus which bears a circuitous sinus.

We call attention to the fact that in the Cambaridae only in *Faxonella clypeata* (Hay, 1899) is the mesial process of the first pleopod of the male greatly reduced and even sometimes absent (see Hobbs 1981: fig. 104b, c). Astounding to us was the observation that also a nearly identical sinus pattern occurs in the annulus ventralis of the two species (see Hobbs 1981:fig. 104d). Is it possible that these secondary sexual features have been developed independently in what we and others have considered to be such disparate species groups?

Associates.—This crayfish is infested with peritrichs and two species of entocytherid ostracods: *Uncinocythere ambophora* (Hobbs & Walton, 1959) and an unidentified member of the genus *Entocythere.* Whereas three copulating pairs of the former were found, only a single female of the latter was retrieved from the sediment in the container in which the crayfish were preserved. The only host that has been reported previously for *U. ambophora* is *P.* (*L.*) *acherontis.*

Etymology.—This crayfish is named in honor of Tom Morris, biologist and cave diver, who collected the type series and provided detailed information on Devil's Sink. Mr. Morris has been working closely with the authors in their survey of the troglobites of Florida and has provided valuable specimens from many otherwise inaccessible (to us) cave sites in the northern part of the state.

Acknowledgments

For their efforts in obtaining the specimens on which the description of this new crayfish is based we extend our thanks to T. Morris and P. Smith. For providing aquarium space to establish a captive population of this troglobite we are indebted to J. D. Williams and the National Fisheries Research Center of the U.S. Fish and Wildlife Service, Gainesville, Florida. We are also grateful to J. F. Fitzpatrick, Jr., of the University of South Alabama, H. H. Hobbs III, of Wittenberg University, and R. B. Manning, of the National Museum of Natural History, for their suggestions and criticisms of the manuscript.

Literature Cited

Cooke, C. Wythe. 1945. Geology of Florida.—Florida Geological Survey Bulletin 29:ix + 339 pp.

Deevey, Edward S. 1988. Estimation of downward leakage from Florida lakes.—Limnology and Oceanography 33(6), Part I:1308–1320.

Franz, Richard, & Shelley E. Franz. 1991. A review of the Florida crayfish fauna, with comments on nomenclature, distribution and conservation.—Florida Scientist (in press).

Hay, William P. 1899. Description of two new species of crayfish.—Proceedings of the United States National Museum 22(1187):121–123.

Hobbs, Horton H., Jr. 1942. A generic revision of the crayfishes of the subfamily Cambarinae (Decapoda, Astacidae) with the description of a new genus and species.—American Midland Naturalist 28(2):334–357.

———. 1972. The subgenera of the crayfish genus *Procambarus* (Decapoda: Astacidae).—Smithsonian Contributions to Zoology 117:1–22.

———. 1981. The crayfishes of Georgia.—Smithsonian Contributions to Zoology 318:viii + 549 pp.

———, & Margaret Walton. 1959. Two new eyeless ostracods of the genus *Entocythere* from Florida.—Quarterly Journal of the Florida Academy of Sciences 22(2):114–120.

Lönnberg, Einar. 1894. Cambarids from Florida, a new blind species.—Zoological Anzeiger 17(444): 125–127.

Pirkle, William A., & E. C. Pirkle. 1984. Physiographic features and field relations of Trail Ridge in northern Florida and southeastern Georgia. Pp. 613–628 *in* A. D. Cohen, D. J. Casagrande, M. S. Andrejko, & G. R. Best, eds., The Okefenokee Swamp: its natural history, geology, and geochemistry. Wetlands Survey, Los Alamos, New Mexico.

(HHH) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (RF) Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 64–75

ADDITIONAL RECORDS OF ENTOCYTHERID OSTRACODS INFESTING BURROWING CRAYFISHES, WITH DESCRIPTIONS OF FIVE NEW SPECIES

Horton H. Hobbs, Jr. and Daniel J. Peters

Abstract.—New records of entocytherids on burrowing crayfishes are recorded from Alabama, Kentucky, Mississippi, Ohio, Tennessee, Virginia, and West Virginia. Represented are species of the genera *Ankylocythere* (5 species), *Ascetocythere* (3), *Dactylocythere* (9), *Donnaldsoncythere* (1), *Lordocythere* (1), *Plectocythere* (1), and *Uncinocythere* (1). New species include *Ankylocythere prolata* from Baldwin County, Alabama, *Dactylocythere guyandottae* from Wyoming County, West Virginia, *Dactylocythere lepta* from Powell County, Kentucky, *Dactylocythere pygidion* from Claiborne County, Tennessee, and *Plectocythere kentuckiensis* from Powell County, Kentucky.

Continued studies of burrowing crayfishes by Raymond F. Jezerinac and G. Whitney Stocker of The Ohio State University, Newark, have disclosed many new records of infestations of entocytherid ostracods and have revealed the existence of five previously undescribed species. Citations of new locality records for species described previously and descriptions of the new ones are presented here. The identities of the host crayfishes were furnished by Messrs. Jezerinac and Stocker.

Except as noted, all of the specimens cited are deposited in the National Museum of Natural History, Smithsonian Institution. References to the original descriptions of the crayfish hosts are omitted from the "Literature Cited" but may be found in Hobbs (1989).

Ankylocythere burkeorum Hobbs III

Ankylocythere burkeorum Hobbs III, 1971: 137, fig. 1a–c.

New record.—Mississippi: Jackson County [Escatawpa Basin], burrows along ditch 2.8 mi (4.5 km) N of Hurley, 2.1 mi (3.4 km) S of Harleston, 22 Mar 1988, Dave Christman, George W. Stocker, and Raymond F. Jezerinac; host: *Cambarus* (*L.*) *ludovicianus* Faxon, 1884; entocytherid associates; none.

Ankylocythere copiosa (Hoff)

Entocythere copiosa Hoff, 1942:69, figs. 9–13.

Ankylocythere copiosa.—Hart, 1962:126.

New record.—Kentucky: Madison County [Kentucky Basin], burrows in wet area at Central Kentucky Wildlife Area, 9.5 mi (15.2 km) SSE of Richmond, 2.7 mi (4.3 km) NE of Bobtown, 26 Mar 1988, G.W.S., D.C., Roger F. Thoma, and R.F.J., host: *Cambarus* (*J.*) *batchi* Schuster, 1973; entocytherid associates; *Dactylocythere macroholca* Hobbs & Hobbs III, 1970, *Uncinocythere simondsi* (Hobbs & Walton, 1960).

Ankylocythere prolata, new species
Fig. 1a–c

Diagnosis.—Male with eye pigmented and located about 0.17 shell length from anterior margin. Shell (Fig. 1b) flattened ventrally, gently arched dorsally and with maximum height slightly posterior to midlength where about 1.3 times height at level of eye; margin entire, lacking emarginations and

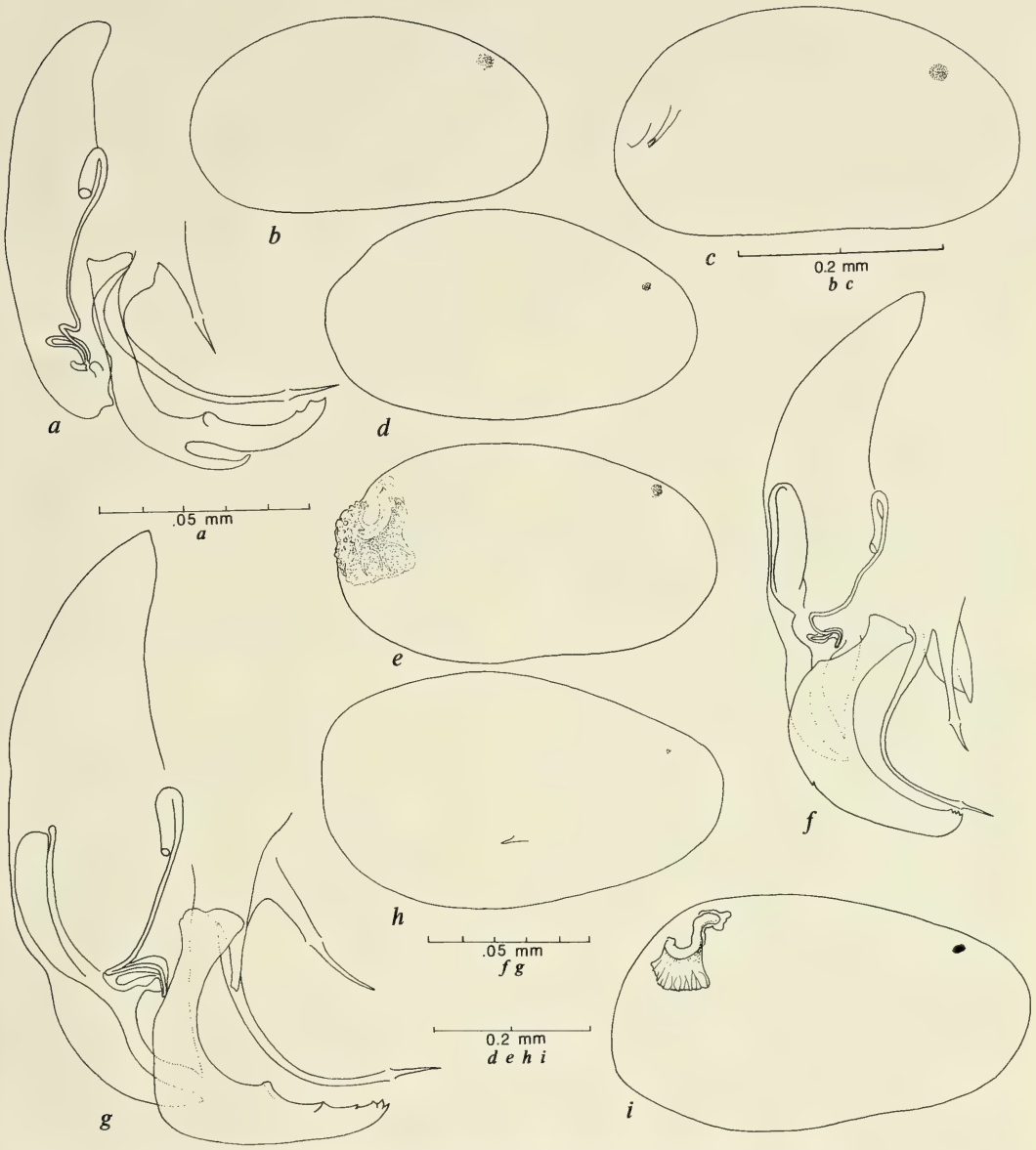


Fig. 1. a–c, *Ankylocythere prolata,* n. sp.; d–f, *Dactylocythere guyandottae,* n. sp.; g–i, *Dactylocythere lepta,* n. sp. (b, d, h, Shell of male; c, e, i, Shell of female; a, f, g, Copulatory complex of male).

prominences. Submarginal setae present except dorsally between level of eye and copulatory complex. Shell length of male 342–357 ($\bar{X}$ = 351) μm; shell height 179–200 ($\bar{X}$ = 186) μm.

Copulatory complex (Fig. 1a) with arched peniferum, rounded ventrally and bearing small subangular prominence near cephaloventral extremity. Clasping apparatus with vertical and horizontal rami subequal in length (or latter longer than former) and disposed at angle of about 103 degrees; vertical ramus almost straight; horizontal one with concave preaxial margin bearing prominent

tooth proximal to midlength and 3 apical denticles; postaxial surface of horizontal ramus with long curved talon arising proximal to large tooth on preaxial border and extending slightly distal to midlength of ramus. Dorsal finger about 0.33 length of ventral finger; latter bent at approximately right angle at end of proximal 0.25, and gently curved in same direction at base of distal 0.40.

Triunguis female.—Eye located about 0.40 shell length from anterior end. Shell (Fig. 1c) very weakly concave ventrally and slightly more highly vaulted than that of male; greatest height slightly posterior to midlength where about 1.2 times that at level of eye. Submarginal setae present except dorsally posterior to eye. Shell length 342–378 ($\bar{X}$ = 366) μm; shell height 207–228 ($\bar{X}$ = 213) μm. Genital papilla long and slender.

Type locality: Crayfish burrows along d'Olide Creek at U.S. Hwy 98, 0.9 mile (1.4 km) south of Bridgehead (the same locality cited by Fitzpatrick 1978:752), Baldwin County, Alabama. The type series was infesting burrowing crayfish collected by D.C., G.W.S., R.F.J., and J. F. Fitzpatrick, Jr.

Disposition of types: The holotypic male and allotypic female are deposited in the National Museum of Natural History (Smithsonian Institution), USNM 235511 and 235512, respectively. Paratypes are in the collections of H. H. Hobbs III and the Smithsonian Institution.

Host: *Cambarus* (*Lacunicambarus*) *miltus* Fitzpatrick, 1978.

Entocytherid associates: None.

Range and specimens examined: Known only from the type locality; seventeen specimens were collected on 22 March 1988 (see "Type locality" above).

Relationships: *Ankylocythere prolata* has its closest affinities with those species possessing a long talon on the horizontal ramus of the clasping apparatus: *A. ancyla* Crawford, 1965; *A. harmani* Hobbs, 1966; *A. hobbsi* Hoff, 1944; and *A. spargosis* Andolshek & Hobbs, 1986. It is readily distinguishable from the last two in that nowhere along its length is the talon bent sharply. It differs from all four of them in that the horizontal and vertical rami are subequal in length or the former is longer than the latter.

Etymology: L. prolatus = prolonged. So named because of the comparatively long horizontal ramus of the clasping apparatus of the male.

Ankylocythere sinuosa (Rioja)

Entocythere sinuosa Rioja, 1942:695, fig. 20.
Ankylocythere sinuosa.—Hart, 1962:127.

New record.—Tennessee: Rhea County [Tennessee Basin], Morgan Creek, 4.0 mi (6.4 km) NW of Dayton, 3 mi (4.8 km) SE of Morgan Springs, 25 Mar 1988, D.C., R.F.T., G.W.S., and R.F.J., host: *Cambarus* (*J.*) sp.?, entocytherid associates: *Dactylocythere astraphyes* Hobbs and Walton, 1977, and *Dt. brachystrix* Hobbs and Walton, 1966.

Ankylocythere tiphophila (Crawford)

Entocythere tiphophila Crawford, 1959:173, figs. 31–37.
Ankylocythere tiphophila.—Hart, 1962:128.

New record.—Tennessee, Campbell County [Clinch Basin], burrows along stream at Cove Lake Park campground, 0.1 mi (0.16 km) N of Caryville, 7.2 mi (11.5 km) SW of La Follette, 12 Aug 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *dubius* Faxon, 1884, entocytherid associate: *Dactylocythere astraphes* Hobbs & Walton, 1977.

Ascetocythere didactylata Hobbs & Hart

Ascetocythere didactylata Hobbs & Hart, 1966:38, figs. 17, 18.

New record.—Tennessee: Claiborne County [Powell Basin], (1) burrows in seep 0.6 mi (0.96 km) N of Riverside, 0.8 mi (1.3 km) SE of poplar Grove, 23 July 1987, G.W.S., D.C., and R.F.J., host: *Cambarus* (*J.*) *dubius,* entocytherid associate: *Dactylo-*

cythere pygidion, new species; (2) burrows adjacent to spring, 10.8 mi (17.3 km) SW of Middlesboro, 2.8 mi (4.5 km) NE of Pleasant, 11 Aug 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *dubius,* entocytherid associates: *Dactylocythere mecoscapha* Hobbs & Walton, 1960, and *Donnaldsoncythere donnaldsonensis* (Klie, 1931).

Ascetocythere sclera Hobbs & Hart

Ascetocythere sclera Hobbs & Hart, 1966: 38, figs. 15, 16.

New records.—Virginia: Highland County [Potomac Basin], burrows along ditch 1.0 mi (1.6 km) SW of Mill Gap, 4.0 mi (6.4 km) WSW of Muscoe, 23 Jun 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *dubius,* entocytherid associate: *Donnaldsoncythere donnaldsonensis.* West Virginia: Clay County [Elk Basin], burrows along ditch 2.5 mi (4 km) NNW of Lizemores, 24.5 mi (39.2 km) E of Charleston, 22 Jun 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *dubius,* entocytherid associates: *Dactylocythere* sp. and *Donnaldsoncythere donnaldsonensis.*

Ascetocythere stockeri Hobbs & Peters

Ascetocythere stockeri Hobbs & Peters, 1989: 325, fig. 1.

New record.—West Virginia: Lincoln County [Guyandotte Basin], burrows along ditch 1.5 mi (2.4 km) NE of Atenville 25 mi (40 km) E of Louisa, 21 Jul 1987, G.W.S., D.C., and R.F.J., host: *Cambarus* (*J.*) *dubius,* entocytherid associate: *Donnaldsoncythere donnaldsonensis.*

Dactylocythere astraphes Hobbs & Walton

Dactylocythere astraphes Hobbs & Walton, 1977:600, fig. 1.

New record.—Tennessee: (1) Campbell County [Clinch Basin], burrows along stream at Cove Lake State Park campground, 0.1 mi (0.2 km) N of Caryville, 7.2 mi (11.5 km) SW of La Follette, 12 Aug 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *dubius,* entocytherid associate: *Ankylocythere tiphophila* (Crawford, 1959). (2) Rhea County [Tennessee Basin], Morgan Creek, 4.0 mi (6.4 km) NW of Dayton, 3.0 mi (4.8 km) SE of Morgan Springs, 25 Mar 1988, D.C., R.F.T., G.W.S., and R.F.J., host: *Cambarus* (*J.*) sp.?, entocytherid associates: *Ankylocythere sinuosa* and *Dactylocythere brachystrix* Hobbs & Walton, 1966.

Dactylocythere brachystrix Hobbs & Walton

Dactylocythere brachystrix Hobbs & Walton, 1966:2, fig. 1a–d.

New record.—Tennessee: Rhea County [Tennessee Basin], Morgan Creek, 4.0 mi (6.4 km) NW of Dayton, 3.0 mi (4.8 km) SE of Morgan Springs, 25 Mar 1988, D.C., R.F.T., G.W.S., and R.F.J., host: *Cambarus* (*J.*) sp.?, entocytherid associates: *Ankylocythere sinuosa,* and *Dt. astraphes.*

Dactylocythere chalaza (Hobbs & Walton)

Entocythere chalaza Hobbs & Walton, 1962: 42, figs. 6–9.
Dactylocythere chalaza.—Hart, 1962:129.

New record.—West Virginia: Greenbrier County [New Basin], burrows along ditch, 0.8 mi (1.3 km) SE of Grassy Meadows, 2.6 mi (4.2 km) S of Dawson, 20 Aug 1988, Tom Jones and G.W.S., host: *Cambarus* (*J.*) *dubius,* entocytherid associates: none.

Dactylocythere crawfordi Hart

Dactylocythere crawfordi Hart, 1965:255, figs. 1, 2.

New record.—Ohio: Auglaize County [Miami Basin], burrows along ditch 1.0 mi (1.6 km) E of Gutman, 2.5 mi (4 km) NW of Santa Fe, 7 Jul 1984, Vicki Stocker and G.W.S., host: *Cambarus* (*L.*) *diogenes* Girard, 1852, entocytherid associate: *Donnaldsoncythere donnaldsonensis.*

Dactylocythere guyandottae, new species
Fig. 1d–f

Diagnosis.—Male with eye located about 0.14 of shell length from anterior end. Shell (Fig. 1d) elliptical, lacking angles, prominences, and emarginations. Submarginal setae sparse but present except dorsally. Shell length of male 428–450 ($\bar{X}$ = 440) μm; shell height 228–250 ($\bar{X}$ = 243) μm. Sternal spine lacking.

Copulatory complex (Fig. 1f) with cephalic margin of peniferum undulating and bowed; apex of ventral extremity sharply acute and directed anteriorly. Accessory groove reaching dorsal extremity of spermatic loop and moderately complex. Clasping apparatus with vertical and horizontal rami joining in broad curve with extremities directed at angle of approximately 85 degrees. Vertical ramus with distinct shoulder on caudal margin and insensibly joined to horizontal ramus; latter without teeth on preaxial border but with unique notch on postaxial border, apical end bearing 4 very small dorsally directed denticles. Finger guard with acute preaxial area and shorter, distally rounded, lamelliform plate flanking it posteriorly.

Triunguis female: Eye located about 0.17 shell length from anterior end. Shell (Fig. 1e) subelliptical with shallow excavation just anterior to midlength; shell length of single female 457 μm; shell height 236 μm. Genital apparatus consisting of J-shaped rod and pendant amiculum supported by few inverted U-shaped rods and slightly protruding from posterior margin of shell.

Type locality: Crayfish burrows in roadside ditch on State Route 971 at Lilydale, 2.2 miles (3.5 km) southwest of Oceana, 3.7 miles (5.9 km) north of Clear Fork, Wyoming County, West Virginia. This locality is in the Guyandotte-Big Sandy River basin.

Disposition of types: The holotypic male and allotypic female are deposited in the National Museum of Natural History (Smithsonian Institution), USNM 235513 and 235519, respectively. Paratypic males are in the collections of H. H. Hobbs III and the Smithsonian Institution.

Hosts: *Cambarus* (*Jugicambarus*) *dubius* and *Cambarus* (*Lacunicambarus*) *diogenes* were preserved in the container from which the type series was obtained. There were no entocytherid associates.

Range and specimens examined: Known only from the type locality where three males and one female were found by G.W.S. and R.F.J. on 6 Jul 1988.

Relationships: Among the closest relatives of this ostracod are *Dt. enoploholca* Hobbs & Walton, 1970, *Dt. isabelae* Hobbs & Peters, 1977, and *Dt. kolura* Hart & Hart, 1971. It differs from the last conspicuously in lacking a caudoventral prominence on the shell and a tooth near midlength of the horizontal ramus of the clasping apparatus. It differs from *Dactylocythere isabelae* in possessing a more robust clasping apparatus, a well defined accessory groove, and a non-bifid finger guard. The chief difference between *Dt. guyandottae* and *Dt. enoploholca* is the lack of teeth on the preaxial border of the clasping apparatus, and a much broader finger guard in the former. It is also the only member of the genus *Dactylocythere* in which a notch is present on the postaxial border of the horizontal ramus of the clasping apparatus.

Etymology: This ostracod bears the name of the Guyandotte River basin where its only known locality is located.

Dactylocythere lepta, new species
Fig. 1g–i

Diagnosis.—Male with eye located about 0.17 shell length from anterior margin, much reduced, represented in some specimens by fewer than a dozen pigment granules. Shell (Fig. 1h) subovate but sometimes with posteroventral angle. Submarginal setae present except dorsally posterior to the eye. Shell length of male 478–514 ($\bar{X}$ = 495) μm; shell height 257–286 ($\bar{X}$ = 272) μm. Sternal spine slender and directed posteriorly.

Copulatory complex (Fig. 1g) with penif-

erum convex posteriorly and with shallow emargination on postaxial margin at level of penis; apex of ventral extremity directed anteriorly. Accessory groove bilobed and reaching about midlength of spermatic loop. Clasping apparatus with vertical and horizontal rami joining at 90 degree angle. Vertical ramus bent at angle of 25 degrees slightly distal to midlength, lacking shoulder on postaxial surface. Horizontal ramus with 3 teeth on preaxial border, proximalmost largest, situated near midlength, penultimate tooth slightly closer to ultimate than to proximal tooth; 3 up-turned apical denticles following ultimate tooth. Finger guard strikingly slender, postaxial border concave; distal extremity subtruncate.

Triunguis female: Eye located about 0.20 shell length from anterior end. Shell (Fig. 1i) larger but otherwise as in male; shell length 493–571 ($\bar{X}$ = 521) μm; shell height 286–328 ($\bar{X}$ = 305) μm. Genital apparatus consisting of slightly tilted S-shaped rod and short amiculum hanging pendant below ventral arm of rod.

Type locality: Crayfish burrows in roadside ditch 2.0 miles (3.2 km) east of State Route 11 on State Route 15, 1.8 miles (2.9 km) east of Slade, Powell County, Kentucky. This locality is in the Kentucky River basin.

Disposition of types: The holotypic male and allotypic female are deposited in the National Museum of Natural History (Smithsonian Institution), USNM 235514 and 235515, respectively. Paratypes are in the collections of H. H. Hobbs III and the Smithsonian Institution.

Host: *Cambarus* (*Jugicambarus*) *dubius.*

Entocytherid associates: *Donnaldsoncythere donnaldsonensis* and *Plectocythere kentuckiensis,* described herein.

Range and specimens examined: Known only from the type locality; 34 specimens were collected from the type locality on 10 Oct 1987 by Paul Matesick, D.C., G.W.S., and R.F.J.

Relationships: *Dactylocythere lepta* probably has its closest affinities with *Dt. astraphes* Hobbs & Walton, 1977, an inhabitant of the Tennessee and Cumberland river basins. Most members of both sexes may be distinguished from those of the latter by the reduced eye spots and subangular posteroventral angle of the shell, the males by the angular, as opposed to straight, vertical ramus of the clasping apparatus, and the females by the S-shaped, instead of long-shanked J-shaped, rod of the genital complex.

Etymology: Gr. Leptos = thin, delicate. So named because of the delicate eye spot and the slender finger guard of the male clasping apparatus.

Dactylocythere macroholca Hobbs & Hobbs

Dactylocythere macroholca Hobbs & Hobbs III, 1970:10, fig. 3a–d.

New record.—Kentucky: Madison County [Kentucky Basin], burrows in wet area in Central Kentucky Wildlife Area, 9.5 mi (15.2 km) SSE of Richmond, 2.7 mi (4.3 km) NE of Bobtown, 26 Mar 1988, G.W.S., D.C., R.F.T., and R.F.J., host: *Cambarus* (*J.*) *batchi*; entocytherid associates: *Ankylocythere copiosa* and *U. simondsi.*

Dactylocythere mecoscapha (Hobbs & Walton)

Entocythere mecoscapha Hobbs & Walton, 1960:19, figs. 17–20.

Dactylocythere mecoscapha.—Hart, 1962: 130.

New records.—Tennessee: Claiborne County [Powell Basin], (1) burrows at spring, 10.8 mi (17.3 km) SW of Middlesboro, 2.8 mi (4.5 km) NE of Pleasant, 11 Aug 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *dubius,* entocytherid associates: *Ascetocythere didactylata* and *Donnaldsoncythere donnaldsonensis.* (2) burrows along tributary to Russell Creek, 6.0 mi (9.6 km) NE of Tazewell, 14.5 mi (23.2 km) SE of Middlesboro, 11 Aug 1987, G.W.S. and R.F.J., hosts: *Cambarus* (*J.*) *dubius* and *Cambarus* (*C.*)

sp., entocytherid associates: *Donnaldsoncythere donnaldsonensis* and *Uncinocythere simondsi.*

Dactylocythere pygidion, new species
Fig. 2d–f

Diagnosis.—Male with well defined eye spot located about 0.14 shell length from anterior margin. Shell (Fig. 2f) ovate with concavity anteroventrally and submarginal setae present except dorsally. Shell length of male 493–536 ($\bar{X}$ = 513) μm; shell height 278–314 ($\bar{X}$ = 291) μm. Sternal spine absent.

Copulatory complex (Fig. 2d) with penifferum bowed posteriorly with faint posterior impression at level just dorsal to penis; apex of ventral extremity directed anteriorly. Accessory groove in form of slender cylinder reaching dorsal margin of spermatic loop. Clasping apparatus with vertical and horizontal rami joining at about 80 degree angle. Vertical ramus only faintly bowed, lacking shoulder on postaxial surface. Horizontal ramus tapering distally, lacking teeth on both pre- and postaxial borders but with 3 apical denticles. Finger guard bearing prominent posteroapical excavation and directed anteroventrally.

Triunguis female: Eye located about 0.29 shell length from anterior end. Shell (Fig. 2e) asymmetrically ovate resulting from posteroventral bulge and posterior notch at level of amiculum; shell length 506–521 ($\bar{X}$ = 514) μm; shell height 278–300 ($\bar{X}$ = 291) μm. Genital apparatus consisting of J-shaped rod and prominent pleated amiculum, part of which hanging pendant and another extending caudoventrally from area of short arm of J-shaped rod and, in part, protruding beyond caudal margin of shell.

Type locality: Seep, 0.1 mile (0.2 km) north of Canoe Branch on Grove Road, 0.6 mile (1 km) north of Riverside; 0.8 mile (1.3 km) southeast of Poplar Grove, Claiborne County, Tennessee. This locality is in the Powell River Basin.

Disposition of types: The holotypic male and allotypic female are deposited in the National Museum of Natural History (Smithsonian Institution), USNM 235516. Paratypes are in the collections of H. H. Hobbs III and the Smithsonian Institution.

Host: *Cambarus* (*Jugicambarus*) *dubius.*

Entocytherid associates: *Ascetocythere didactylata.*

Range and specimens examined: Known only from the type locality; 17 specimens were collected on 23 Jul 1987 by G.W.S., D.C., and R.F.J.

Relationships.—Among its closely allied congeners *Dactylocythere pygidion* seems to be more similar to *Dt. falcata* Hobbs and Walton, 1961, than to *Dt. corvus* Hobbs and Walton, 1977, *Dt. myura* Hobbs and Walton, 1970, and *Dt. prominula* Hobbs and Walton, 1977. Despite the similarities, it differs from *Dt. falcata* in possessing a simple accessory groove that extends dorsally only to the dorsal level of the spermatic loop, and there are three terminal denticles at the apex of the clasping apparatus. In *Dt. falcata* the complex accessory groove extends considerably dorsal to the spermatic loop, and the apex of the clasping apparatus usually lacks denticles.

Etymology: Gr. Pygidion = rump. So named because of the prominent posteroventral prominence on the shell of all of the females and a hint of such in some of the males.

Donnaldsoncythere donnaldsonensis (Klie)

Entocythere donnaldsonensis Klie, 1931: 334, figs. 1–9.

Donnaldsoncythere donnaldsonensis.—Hart, 1962:131.

New records.—Kentucky: Powell County [Kentucky Basin], burrows along ditch 1.8 mi (2.9 km) E of Slade, 2.7 mi (4.3 km) NW of Pine Ridge, 10 Oct 1987, P.M., D.C., G.W.S., and R.F.J., host: *Cambarus J.*) *dubius,* entocytherid associates: *Dactylo-*

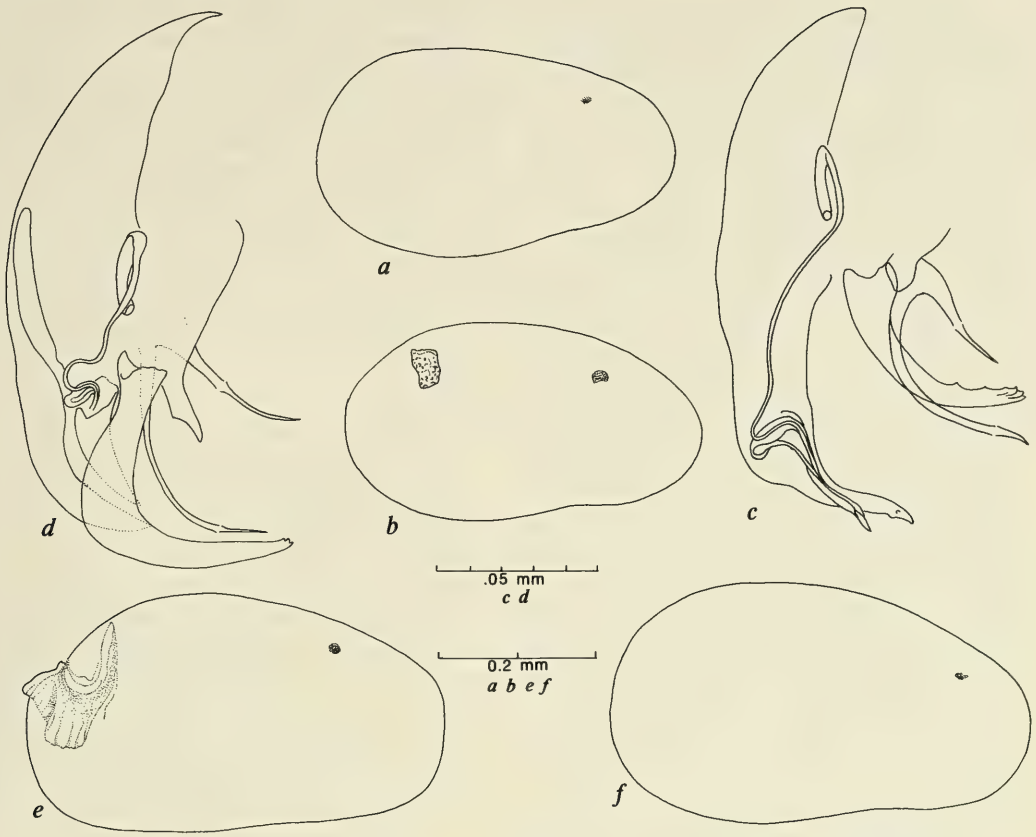


Fig. 2. a–c, *Plectocythere kentuckiensis,* n. sp.; d–f, *Dactylocythere pygidion,* n. sp. (a, f, Shell of male; b, e, Shell of female; c, d, Copulatory complex of male).

cythere lepta and *Plectocythere kentuckiensis,* new species.

Ohio: Augalaize County [Miami Basin], burrows along ditch 1.0 mi (1.6 km) E of Gutman, 2.5 mi (4 km) NW of Santa Fe, 7 Jul 1984, V.S. and G.W.S., host: *Cambarus* (*L.*) *diogenes,* entocytherid associate: *Dactylocythere crawfordi.*

Tennessee: Claiborne County [Powell Basin], (1) burrows at spring 10.8 mi (17.3 km) SW of Middlesboro, 2.8 mi (4.5 km) NE of Pleasant, 11 Aug 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *dubius,* entocytherid associates: *Ascetocythere didactylata* and *Dactylocythere mecoscapha.* (2) burrows along tributary to Russell Creek, 6.0 mi (9.6 km) NE of Tazewell, 14.5 mi (23.2 km) SE of Middlesboro, 11 Aug 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *dubius* and *C.* (*C.*) sp.?, entocytherid associates: *Dactylocythere mecoscapha* and *Uncinocythere simondsi.*

Virginia: Highland County [Potomac Basin], (1) burrows along ditch 1.0 mi (1.6 km) SW of Mill Gap, 4.0 mi (6.4 km) WSW of Mustoe, 23 Jun 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *dubius,* entocytherid associate: *Ascetocythere sclera.* (2) burrows at spring 1.5 mi (2.4 km) E of Monterey, 5.0 mi (8 km) NE of Vanderpool, 24 Jun 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *monongalensis* Ortmann, 1905, entocytherid associate: none.

West Virginia: (1) Clay County [Elk Ba-

sin], burrows along ditch 2.5 mi (4 km) NNW of Lizemores, 24.5 mi (39.2 km) E of Charleston, 22 Jun 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *dubius,* entocytherid associates: *Ascetocythere sclera* and *Dactylocythere* sp.? (2) Greenbrier County (Kanawha Basin), burrows along ditch at Summit Lake National Forest campground, 6 mi (9.6 km) ENE of Richwood, 13.0 mi (20.8 km) SE of Cowen, 23 Jun 1987, G.W.S. and R.F.J., hosts: *Cambarus* (*C.*) *cavatus* Hay, 1902, *C.* (*J.*) *dubius,* and *C.* (*J.*) *monongalensis,* entocytherid associates: none. (3) Greenbrier County [New Basin], burrows at cave on U.S. Hwy 219, 1.25 mi (2 km) SW of Renick, 2.5 mi (4 km) NW of Spring Creek, 20 Aug 1988, T.J. and G.W.S., host: *Cambarus* (*P.*) *nerterius,* Hobbs, 1964, entocytherid associate: *Uncinocythere simondsi.* (4) Kanawha County [Kanawha Basin], burrows along ditch 3.5 mi (5.6 km) NW of Delva, 22.0 mi (35.2 km) SE of Charleston, 22 Jun 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *dubius,* associates: none. (5) Lincoln County [Guyandotte Basin], burrows in seep 1.5 mi (2.4 km) NE of Atenville, 25.0 mi (40 km) E. of Louisa, 21 Jul 1987, G.W.S., D.C., and R.F.J., host: *Cambarus* (*J.*) *dubius,* associate: *Ascetocythere stockeri.* (6) Monroe County [Kanawha Basin], burrows along ditch 0.1 mi (0.2 km) NW of Gap Mill, 1.0 mi (1.6 km) SE of Red Mill, 18 Aug 1988, T.J. and G.W.S., host: *Cambarus* (*J.*) *dubius,* associates: none. (7) Pocahontas County [Kanawha Basin], seep 4.9 mi (7.8 km) NW of Woodrow, 9.7 mi (15.5 km) NW of Marlington, 23 Jun 1987, G.W.S. and R.F.J., hosts: *Cambarus* (*C.*) *carinirostris* and *Cambarus* (*J.*) *monongalensis,* associates: none. (8) Pocahontas County [Kanawha Basin], ditch and seep 1.0 mi (1.6 km) S of Thornwood, 3.2 mi (5.1 km) E of Barton, 23 Jun 1987, G.W.S. and R.F.J., hosts: *Cambarus* (*C.*) *carinirostris* and *C.* (*J.*) *monongalensis,* associates: none. (9) Pocahontas County [Kanawha Basin], burrows along ditch at Arbovale, 1.5 mi (2.4 km) NNE of Greenbank, 23 Jun 1987, G.W.S. and R.F.J., hosts: *Cambarus* (*J.*) *dubius* and *C.* (*J.*) *monongalensis,* associates: none. (10) Tucker County [Monongahela Basin], seep 0.1 mi (0.2 km) N of Gladwin, 9.2 mi (14.7 km) SE of Parsons, 26 Jun 1987, G.W.S. and R.F.J., host: *Cambarus* (*J.*) *monongalensis,* associates: none. (11) Wyoming County [Guyandotte Basin], burrows in ditch along St. Rte. 971 at Lilydale, 6 Jul 1988, G.W.S. and R.F.J., hosts: *Cambarus* (*J.*) *dubius* and *C.* (*L.*) *diogenes,* entocytherid associate: *Dactylocythere guyandottae.*

Lordocythere petersi Hobbs & Hobbs

Lordocythere petersi Hobbs & Hobbs III, 1970:16, fig. 9.

New record.—Tennessee: Morgan County [Tennessee Basin], burrows in ditch at Petros-Joiner School yard, 1.5 mi (2.4 km) W of Union, 11.1 mi (17.8 km) WNW of Oak Ridge, 24 July 1987, D.C., G.W.S. and R.F.J., host: *Cambarus* (*L.*) *acanthura* Hobbs, 1981, entocytherid associates: none.

Plectocythere kentuckiensis, new species
Fig. 2a–c

Diagnosis.—Male with eye spots reduced and located about 0.25 shell length from anterior margin. Shell (Fig. 2a) ovate with broad shallow concavity ventrally about level of eye spot. Submarginal setae present except dorsally. Shell length 440–493 ($\bar{X}$ = 448) μm; shell height 250–278 ($\bar{X}$ = 263) μm.

Copulatory complex (Fig. 2c) with ventral part of peniferum very slightly swollen and produced in tapering slender, gently undulating projection terminating in 3 tuberculiform prominences; penis emerging from digitiform extension borne on projection near its base; neither prostatic or spermatic element of penis as long as clasping apparatus. Clasping apparatus forming gentle arc, not divisible into horizontal and vertical rami; postaxial border entire; preaxial bor-

der with 3 subequally-spaced teeth in distal third, apex bearing 3 terminal denticles. Ventral finger about twice as long as dorsal finger and gently curved along proximal three-fifths.

Triunguis female.—Eye weakly pigmented and situated 0.26 shell length from anterior margin (Fig. 2b). Shell ovate with shallow ventral concavity in anterior half sometimes more conspicuous than that in male. Submarginal setae present except dorsally. Shell length 457–478 ($\bar{X}$ = 469) μm; shell height 250–278 ($\bar{X}$ = 265) μm. Genital apparatus consisting of hyaline globular mass covered with brown, presumably foreign, finely-particulate matter.

Type locality: Crayfish burrows in roadside ditch 2.0 miles (3.2 km) east of State Route 11 on State Route 15, 1.8 miles (2.9 km) E of Slade, Powell County, Kentucky. This locality is in the Kentucky River basin.

Disposition of types: The holotypic male and allotypic female are deposited in the National Museum of Natural History (Smithsonian Institution), USNM 235517 and 235518, respectively. Paratypes are in the collections of H. H. Hobbs III and the Smithsonian Institution.

Host: *Cambarus* (*Jugicambarus*) *dubius.*

Entocytherid associates: *Donnaldsoncythere donnaldsonensis* and *Dactylocythere lepta,* described above.

Range and specimens examined: Known only from the type locality. Thirteen specimens (9 males and 4 females) were obtained from the crayfish collected on 10 Oct 1987 by P.M., D.C., G.W.S., and R.F.J.

Relationships: *Plectocythere kentuckiensis* is the fourth species to be assigned to this genus, the range of which is circumscribed by four localities in Kentucky: two in Bell County (the type localities of *P. crotaphis* Hobbs III, 1965, and *P. odelli* Norden, 1977), one in Letcher County (the type locality of *P. johnsonae* Hobbs & Hart, 1966), and that cited above in Powell County. They also infest the same host, *Cambarus* (*Jugicambarus*) *dubius* (*Cambarus carolinus.*—Hobbs & Hart, 1966, and Hobbs III, 1969, =*Cambarus* (*J.*) *dubius*). These are closely allied forms, and which of the three is most closely allied to *P. kentuckiensis* is problematical. The undulating ventral extension of the peniferum resembles that in *P. crotaphis* and *P. odelli* more closely than it does that of *P. johnsonae* which is only slightly curved, but the undulation is much weaker in *P. kentuckiensis,* and whereas in *P. crotaphis* and *P. odelli* the extension is directed caudally, that in *P. kentuckiensis* is disposed caudoventrally. Moreover the prominence from which the penis emerges originates at the base of the extension, much proximal to its tip. Three features of *P. kentuckiensis* seem to be unique in the species group: both the spermatic and prostatic elements of the penis are shorter than the clasping apparatus; the terminal end of the peniferal extension bears 2 or 3 small tuberculiform lobes; and the teeth and apical denticles on the clasping apparatus are sharply defined and clearly positioned on the postaxial border of the apparatus.

Uncinocythere simondsi
(Hobbs & Walton)

Entocythere simondsi Hobbs & Walton, 1960:17, figs. 1–10.
Uncinocythere simondsi.—Hart, 1962:123.

New record.—Kentucky: Madison County [Kentucky Basin], burrows at Central Kentucky Wildlife Area, 9.5 mi (15.2 km) SSE of Richmond, 2.7 mi (4.3 km) NE of Bobtown, 26 Mar 1988, G.W.S., D.C., R.F.T., and R.F.J., host: *Cambarus* (*J.*) *batchi,* entocytherid associates: *Ankylocythere copiosa* and *Dactylocythere macroholca.*

Tennessee: Claiborne County [Powell Basin] burrows along tributary to Russell Creek, 6.0 mi (9.6 km) NE of Tazewell, 14.5 mi (23.2 km) SE of Middlesboro, 11 Aug 1987, G.W.S. and R.F.J., hosts: *Cambarus* (*C.*) sp.? and *C.* (*J.*) *dubius,* entocytherid associates: *Dactylocythere mecoscapha* and *Donnaldsoncythere donnaldsonensis.*

West Virginia: Greenbrier County [Kanawha Basin], cave on U.S. Hwy 219, 1.25 mi (2.0 km) SW of Renick, 2.5 mi (4 km) NW of Spring Creek, 20 Aug 1988, T.J. and G.W.S., host: *Cambarus (P.) nerterius,* entocytherid associate: *Donnaldsoncythere donnaldsonensis.*

Acknowledgments

Thanks are extended to Raymond F. Jezerinac and G. Whitney Stocker for providing the material on which this study is based as well as the identities of the crayfish hosts. We are also grateful to Thomas E. Bowman of the Smithsonian Institution, H. H. Hobbs III, of Wittenberg University, and Raymond Jezerinac for their criticisms of the manuscript.

Literature Cited

Andolshek, Margaret D., & Horton H. Hobbs, Jr. 1986. The entocytherid ostracod fauna of southeastern Georgia.—Smithsonian Contributions to Zoology 424:1–43.

Crawford, E. A., Jr. 1959. Five new ostracods of the genus *Entocythere* (Ostracoda, Cytheridae) from South Carolina.—University of South Carolina Publications, Biology, Series III 2(4):149–189.

———. 1965. Three new species of epizoic ostracods (Ostracoda, Entocytheridae) from North and South Carolina.—American Midland Naturalist 74(1):148–154.

Fitzpatrick, J. F., Jr. 1978. A new burrowing crawfish of the genus *Cambarus* from southwest Alabama (Decapoda, Cambaridae).—Proceedings of the Biological Society of Washington 91:748–755.

Hart, C. W., Jr. 1962. A revision of the ostracods of the family Entocytheridae.—Proceedings of the Academy of Natural Sciences of Philadelphia 114(3):121–147.

———. 1965. New entocytherid ostracods and distribution records for five midwestern states.—Transactions of the American Microscopical Society 84(2):255–259.

———, & Dabney G. Hart. 1971. New entocytherid ostracods of the genera *Ankylocythere, Dactylocythere, Entocythere, Geocythere,* and *Uncinocythere*—with a new diagnosis of the genus *Entocythere.*—Proceedings of the Academy of Natural Sciences of Philadelphia 123(5):105–125.

Hobbs, Horton H., Jr. 1966. An illustrated key to the species of the genus *Ankylocythere* with description of a new species from Louisiana (Ostracoda, Entocytheridae).—Proceedings of the Louisiana Academy of Sciences 29:67–75.

———. 1989. An illustrated checklist of the American crayfishes (Decapoda: Astacidae, Cambaridae, and Parastacidae).—Smithsonian Contributions to Zoology 480:iii + 236 pp.

———, & C. W. Hart, Jr. 1966. On the entocytherid ostracod genera *Ascetocythere, Plectocythere, Phymocythere* (gen. nov.), and *Cymocythere* with descriptions of new species.—Proceedings of the Academy of Natural Sciences of Philadelphia 118(2):35–61.

———, & H. H. Hobbs III. 1970. New entocytherid ostracods with a key to the genera of the subfamily Entocytherinae.—Smithsonian Contributions to Zoology 47:1–19.

———, & Daniel J. Peters. 1977. The entocytherid ostracods of North Carolina.—Smithsonian Contributions to Zoology 247:iv + 73 pp.

———, & ———. 1989. New records of entocytherid ostracods infesting burrowing crayfishes, with the description of a new species, *Ascetocythere stockeri.*—Proceedings of the Biological Society of Washington 102:324–330.

———, & Margaret Walton. 1960. Three new ostracods of the genus *Entocythere* from the Hiwassee drainage system in Georgia and Tennessee.—Journal of the Tennessee Academy of Sciences 35(1):17–23.

———, & ———. 1961. Additional new ostracods from the Hiwassee drainage system in Georgia, North Carolina, and Tennessee.—Transactions of the American Microscopical Society 80(4): 379–384.

———, & ———. 1962. New ostracods of the genus *Entocythere* from the Mountain Lake region, Virginia (Ostracoda, Entocytheridae).—Virginia Journal of Science 13(2):42–48.

———, & ———. 1966. A new genus and six new species of entocytherid ostracods (Ostracoda, Entocytheridae).—Proceedings of the United States National Museum 119(3542):1–12.

———, & ———. 1970. New entocytherid ostracods from Tennessee and Virginia.—Proceedings of the Biological Society of Washington 82(68):851–864.

———, & ———. 1977. New entocytherid ostracods of the genus *Dactylocythere.*—Proceedings of the Biological Society of Washington 90(3):600–614.

Hobbs H. H., III. 1965. Two new genera and species of the ostracod family Entocytheridae, with a key to the genera.—Proceedings of the Biological Society of Washington 78(19):159–164.

———. 1969. A new genus and two new species of

entocytherid ostracods from Alabama and Mississippi.—Proceedings of the Biological Society of Washington 82(10):167–170.

———. 1971. New entocytherid ostracods of the genera *Ankylocythere* and *Dactylocythere*.—Proceedings of the Biological Society of Washington 84(17):137–146.

Hoff, C. Clayton. 1942. The subfamily Entocytherinae, a new subfamily of freshwater cytherid ostracods, with descriptions of two new species of the genus *Entocythere*.—American Midland Naturalist 27(1):63–73.

———. 1944. New American species of the ostracod genus *Entocythere*.—American Midland Naturalist 32(2):327–357.

Klie, W. 1931. Campagne spéologique de C. Bolivar et R. Jeannel dans l'Amérique du Nord (1928) 3: Crustacés Ostracodes.—Biospéologica: Archives de Zoologie Expérimentale et Générale 71(3):333–344.

Norden, Arnold W. 1977. A new entocytherid ostracod of the genus *Plectocythere*.—Proceedings of the Biological Society of Washington 90:491–494.

Rioja, Enrique. 1942. Descripción de una especie y una subspecie nuevas del género *Entocythere* Marshall, precedentes de la Cueva Chica (San Luis Potosí, México).—Ciencia (México) 3(7): 201–204.

(HHH) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (DJP) York High School, 9300 George Washington Highway, Yorktown, Virginia 23692.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 76–90

REDESCRIPTION OF TWO SPECIES OF *PSEUDIPHIMEDIELLA* FROM THE SOUTHERN OCEAN (AMPHIPODA: IPHIMEDIIDAE)

C. O. Coleman and J. L. Barnard

Abstract.—*Pseudiphimediella nodosa* and *P. glabra* are redescribed from previously unreported materials and compared together taxonomically. Variability is discussed.

A review of *Pseudiphimediella,* with new diagnosis, and redescription of the two known species of the genus, is based on newly examined specimens in the collections of Smithsonian Institution.

Iphimediidae

Pseudiphimediella Schellenberg

Pseudiphimediella Schellenberg, 1931: 119 (*Amphitoe nodosa* Dana, 1853, original designation).—Watling & Holman, 1980: 639.

Diagnosis.—Body covered with teeth or processes. Antenna 1: peduncular article 2 shorter than 1. Mouthparts projecting quadrately. Labrum incised, not very broad. Mandibular incisor broad, cutting frontally, weakly toothed; raker row absent; molar absent. Lower lip: inner lobes absent. Maxilla 1: palp 2-articulate, article 2 ordinary. Maxilla 2: inner plate without facial row of setae. Maxillipeds: inner plate as long but not as broad as outer plate, palp article 2 broad and apicomedially unproduced; palp article 4 obsolescent. Coxae ordinary. Gnathopods scarcely diverse, of slightly different sizes, articles 5–6 elongate, narrow; both gnathopods chelate; gnathopod 2 more strongly setose than 1. Telson scarcely incised.

Relationship.—Like *Iphimediella* but mandible cutting in frontal plane; thus mouthparts projecting quadrately.

Differing from *Echiniphimedia* in the absence of surficial cusps, all teeth emerging from margins of segments and coxae.

Species.—(Geographic codes in brackets are explained in Barnard & Barnard, 1983: 181); *P. glabra* (Schellenberg, 1931), bathyal Falkland-Magellan region [866 + B]; *nodosa* (Dana, 1853) (Barnard, 1932), Falkland-Magellan region [866].

Distribution.—Marine, Magellanic region and Falkland Islands, 0–494 m, 2 species.

Pseudiphimediella nodosa (Dana, 1853) Figs. 1–5

Iphimedia nodosa Dana, 1853:928, pl. 63, fig. 3A, B.—?Stebbing, 1906:216.

Pseudiphimediella nodosa: Schellenberg, 1931:119, fig. 64, pl. 1, fig. A.

?*Iphimediella nodosa*: K. H. Barnard, 1932: 119, fig. 67; non K.H. Barnard, 1930:361 (=*Echiniphimedia echinata*).

Pseudiphimediella nodosa: Watling & Holman, 1980:641, fig. 21.

Material.—Ovigerous female (32 eggs), 10.5 mm, # 76 (W.L.S[chmitt].); Punta Arenas, Chile; 4 Feb 1927.

Description.—Body (Fig. 1a, d): Robust, pereon increasing in width to fifth pereonite; pereonite 2 shortest; pereonite 5 with pair of blunt teeth posteromarginally, on pereonite 6 longer and acute teeth; pereonite 7 with 4 posteromarginal teeth, middorsal pair longer and stout, posteroventral corner of pereonite 7 pointed; metasomites 1–2 with

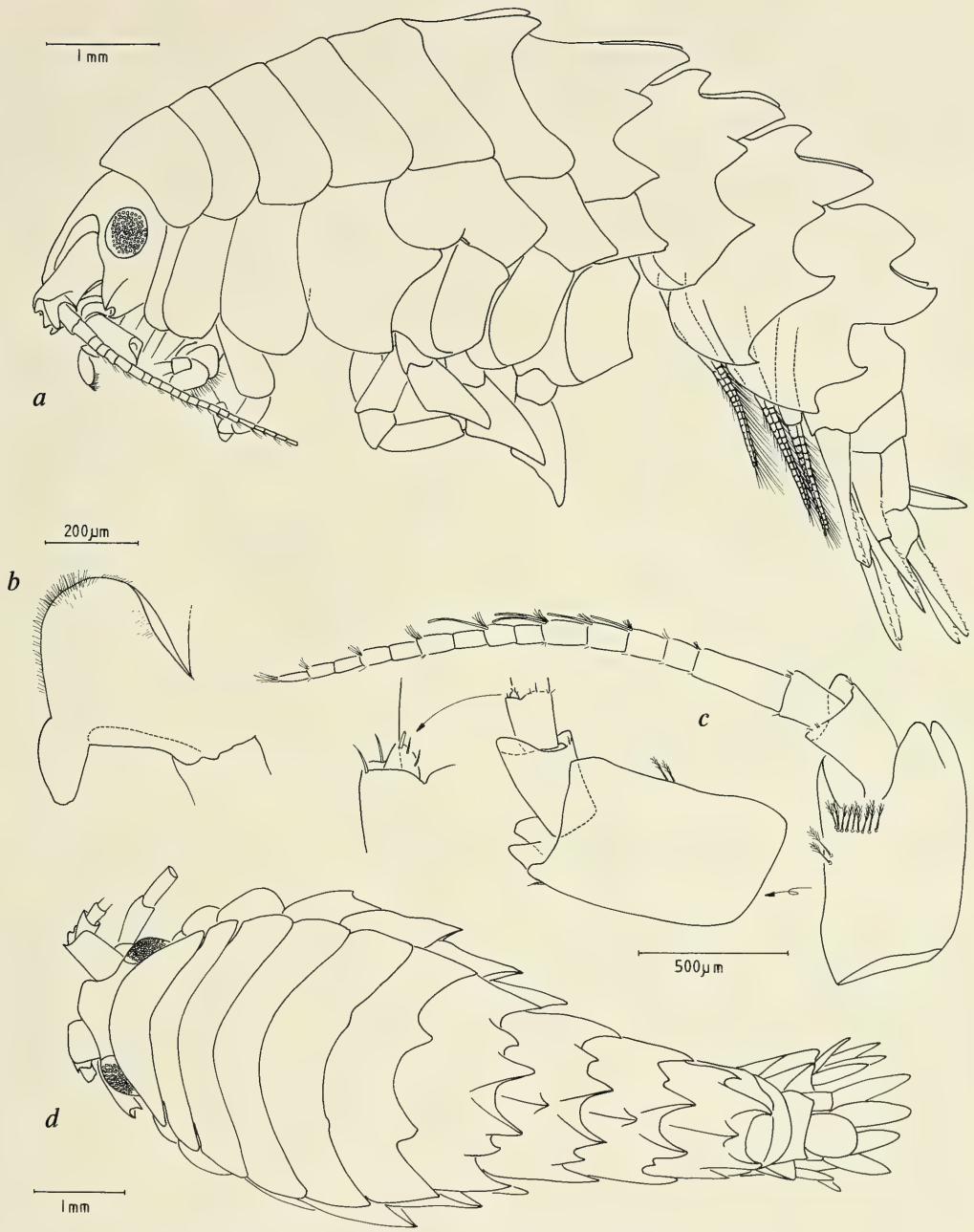


Fig. 1. a–d, *Pseudiphimediella nodosa* female. a, lateral view of habitus. b, labium (lower lip). c, antenna 1. d, dorsal view of habitus.

similar posteromarginal teeth and middorsal tooth; epimeron 1 shorter than 2 and 3; metasomite 3 with elongate middorsal tooth and 2 stout teeth posteromarginally; all metasomites with acute processes laterally; posteroventral angles of epimera 2 and 3 acute; urosomite 1 with dorsal hump; urosomite 2 shortest.

Head: Eyes round, rostrum strongly curved ventrally; lateral cephalic lobe notched and ridged.

Antenna 1 (Fig. 1c): Shorter than antenna 2; peduncular article 1 stout, with 3 processes and plumose setae apically; article 2 slender, slightly expanded distally; article 3 shortest; accessory flagellum uniarticulate, scale-like; 14 flagellar articles, flagellar article 1 longest.

Antenna 2 (Fig. 2c, f): Peduncular article 1 with acute process; article 2 with short gland cone; article 3 shorter than article 1, subequal in length to article 2; article 4 with 2 processes apically, slightly expanded distally; article 5 subequal in length to 4; flagellum consisting of 32 articles, each with group of short setae apically.

Labrum (Fig. 2a): Broad, incised, symmetrically lobed.

Mandible (Fig. 2b, e): Incisors dentate, molar and rakers absent; lacinia mobilis of left mandible broad, apically dentate; lacinia mobilis of right mandible slender, pointed; mandibular palp 3-articulate, article 1 shortest; article 2 longest, with 3 long setae laterodistally.

Lower lip (Fig. 1b): Lobes broad, unnotched, apically setose; mandibular process rounded.

Maxilla 1 (Fig. 2g): Inner lobe shorter than outer lobe, with 7 setulated setae marginally; outer plate slender, with 9 medially dentate setae apically; palp 2-articulate, broad, article 2 twice as long as 1 with 2 rows of setae apically.

Maxilla 2 (Fig. 2d): Inner lobe wider than outer lobe, subequal in length, setae as in detail of Fig. 2d; inner lobe long setae apically.

Maxilliped (Fig. 3d–g): Inner lobes long, apically truncate, with setulated setae mediomarginally and apically; outer plate broad, rounded, with long setulated setae lateromarginally and shorter setae mediomarginally; palp 3-articulate, articles 1 and 2 broad, article 2 slightly produced medially, article 3 slender, apically with small peg; palp densely setose (in Fig. 3e only the places of insertion of setae are shown, dotted line indicating maximal length of setae).

Gnathopod 1 (Fig. 3c): Shorter than gnathopod 2; coxa tapering distally; basis elongate, narrowing distally, slightly sinuous anteromarginally, with some setae on lateral face and anteromarginally; ischium longer than merus; carpus slender, shorter than propodus; chela as in detail of Fig. 3c.

Gnathopod 2 (Fig. 3a, b): Coxa apically truncate; basis elongate; ischium longer than merus; carpus slightly excavate anteriorly, with anteromarginal setae; carpus and propodus subequal in length; propodus with groups of setae anteromarginally, propodus with broad apical process and slender dactylus forming chela (Fig. 3b).

Pereopod 3 (Fig. 4a): Coxa broad, rounded apically; basis longer than ischium and merus combined; ischium shortest; merus expanded distally, with anteroapical process; carpus subequal in length to merus; propodus longer than carpus; dactylus with apical claw.

Pereopod 4 (Fig. 4b): Coxa rounded anteriorly, with subacute process posteriorly; basis to dactylus as for pereopod 3.

Pereopod 5 (Fig. 4c): Coxa wider than long, rounded anteriorly, subacutely processed posteriorly; basis broad, ridged, slightly excavate posteriorly, deeply excavate ventrally; some spiniform setae anteriorly; ischium short, partly hidden by basis, slightly projecting anteriorly; merus expanded distally, with acute process posteriorly.

Pereopod 6 (Fig. 4d): Coxa of similar shape as pereopod 5, but posterior process pointed acutely; basis subequal to pereopod 5, but slightly longer and with more spiniform setae anteromarginally; ischium and merus subequal to pereopod 5, but posterodistal process longer.

Pereopod 7 (Fig. 5a): Coxa smallest, subacutely produced posteriorly; basis longer

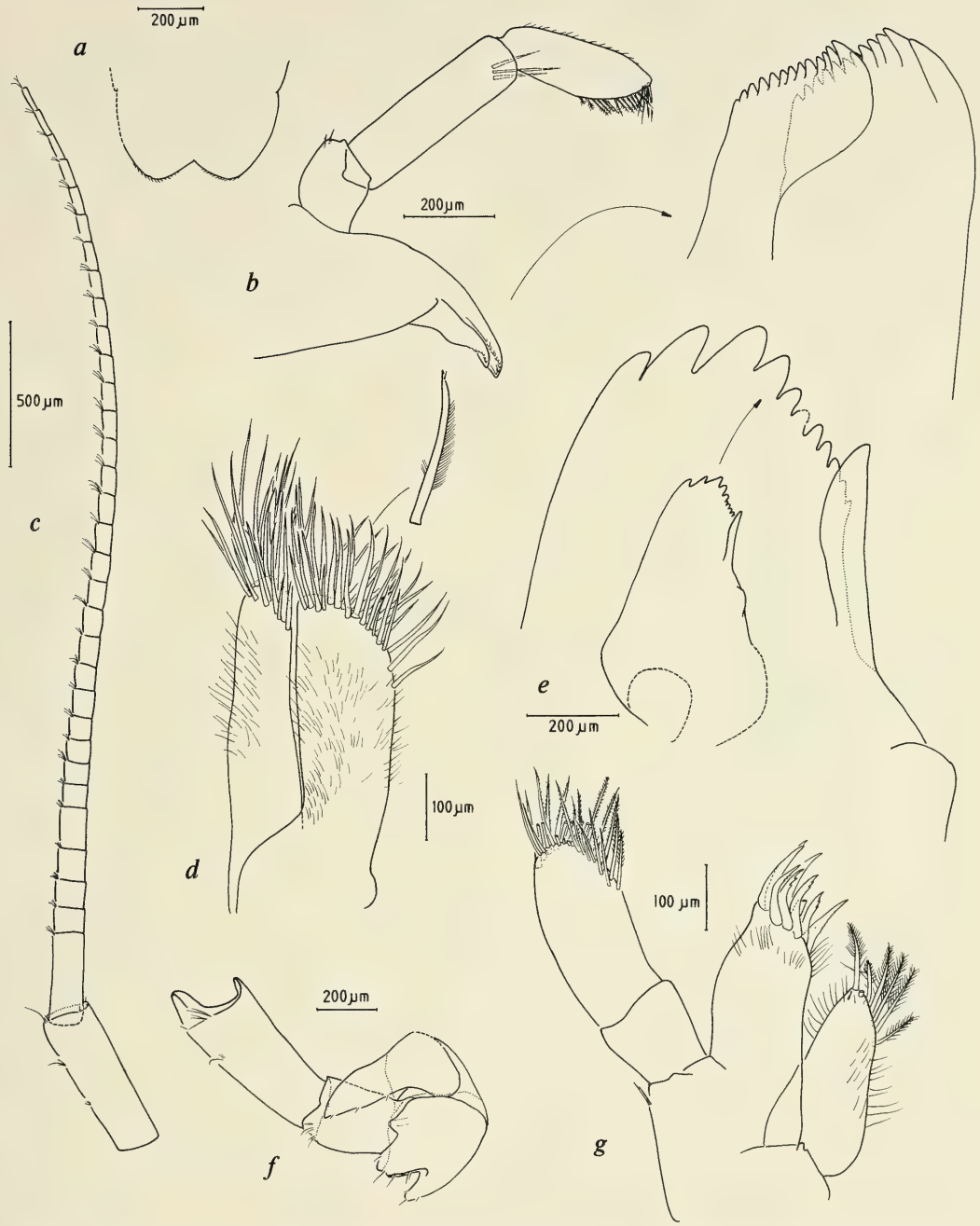


Fig. 2. a–g, *Pseudiphimediella nodosa* female. a, labrum (upper lip). b, left mandible, detail showing medial view of incisor region and lacinia mobilis. c, peduncular article 5 and flagellum of antenna 2. d, maxilla 2. e, right mandible, detail showing incisor and lacinia mobilis. f, peduncular articles 1–4 of antenna 2. g, maxilla 1.

Fig. 3. a–g, *Pseudiphimediella nodosa* female. a, gnathopod 2. b, chela of pereopod 2. c, gnathopod 1, detail showing chela. d, inner plate of maxilliped. e, maxillipedal palp, setae partly omitted, place of insertion shown, dotted line indicating length of setae. f, maxilliped seen from oral side, setae omitted. g, outer plate of maxilliped, setae partly omitted with places of insertion of lateromarginal setae shown.

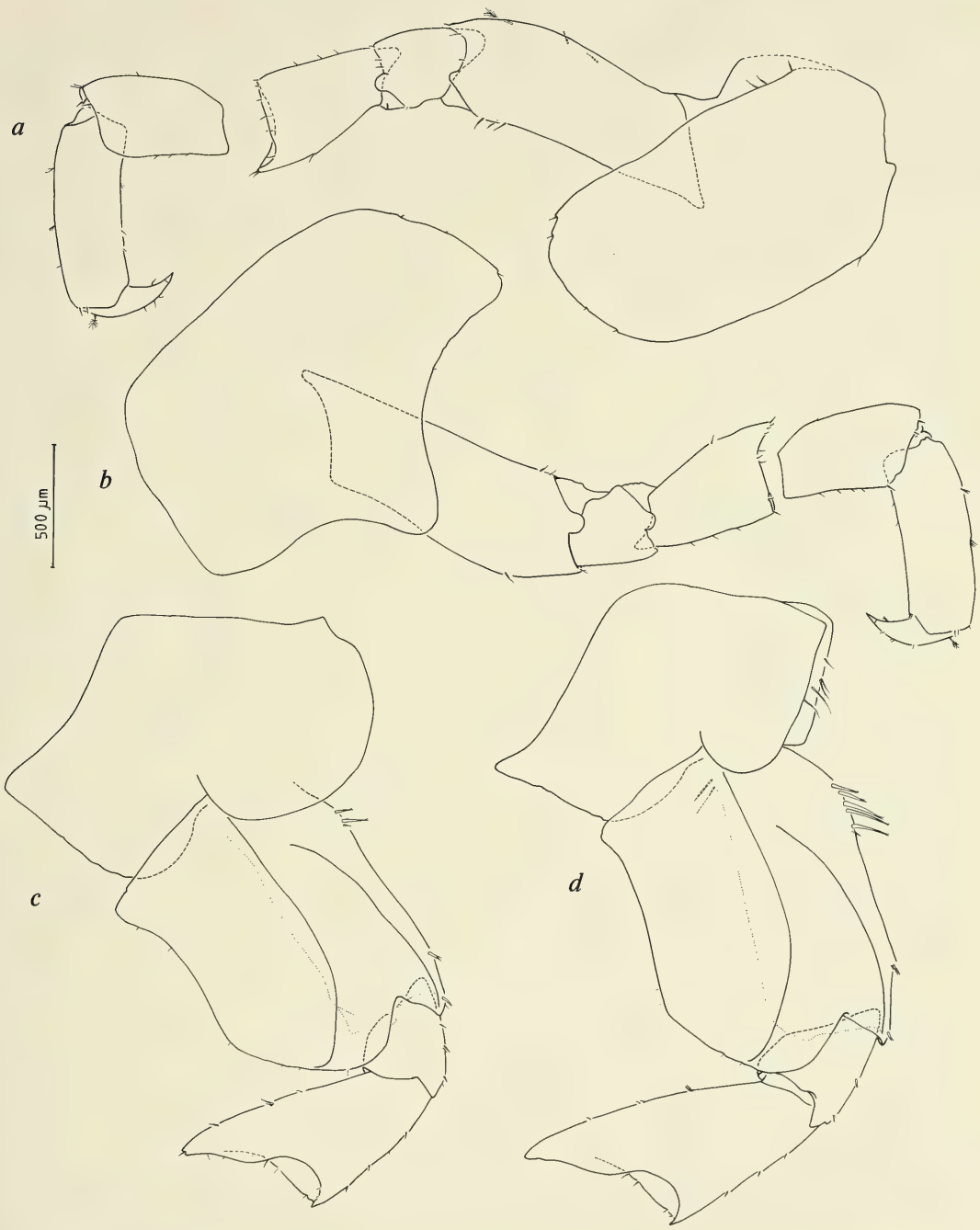


Fig. 4. a–d, *Pseudiphimediella nodosa* female. a, pereopod 3. b, pereopod 4. c, pereopod 5. d, pereopod 6.

and wider compared to pereopod 6, slightly excavate posteromarginally, forming 2 short processes; ischium and merus as for pereopod 6.

Pleopod 1 (Fig. 5b): Peduncle relatively broad, with lateral setulated setae; inner ramus slightly longer; 2 coupling hooks as in detail of Fig. 5b.

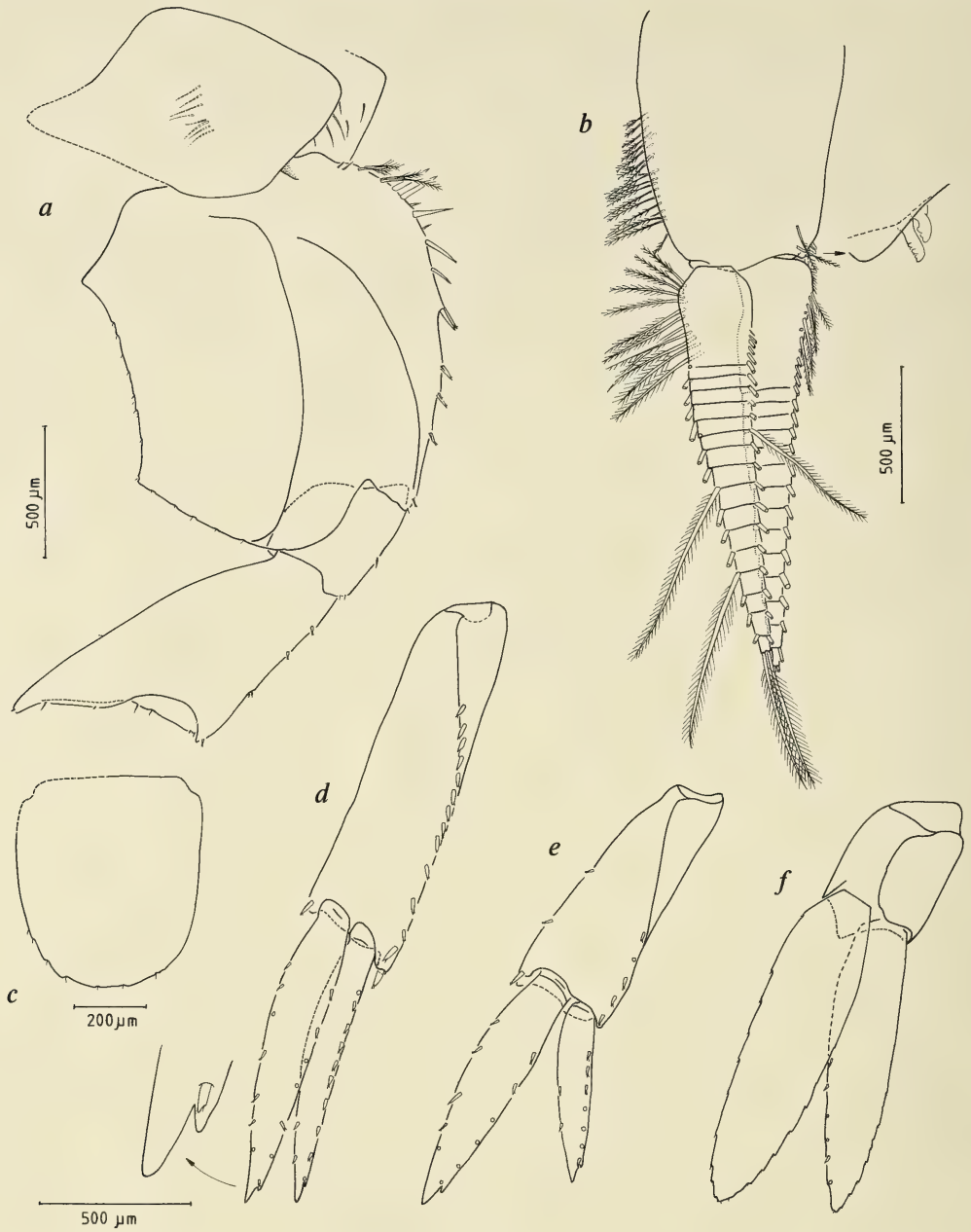


Fig. 5. a–f, *Pseudiphimediella nodosa* female. a, pereopod 7, coxa damaged posteriorly. b, pleopod 1. c, telson. d, uropod 1. e, uropod 2. f, uropod 3.

Uropod 1 (Fig. 5d): Peduncle longer than rami; rami subequal in length, apically bifid asymmetrically as in detail of Fig. 5d.

Uropod 2 (Fig. 5e): Shorter than uropod 1; peduncle slightly shorter than inner ramus; outer ramus shorter than inner ramus; in lateral view tips of rami not reaching apices of uropods 1 and 3.

Uropod 3 (Fig. 5f): Peduncle much shorter than rami; rami subequal in length, inner ramus wider, lanceolate and without spiniform setae.

Telson (Fig. 5c): Longer than wide, distally rounded.

Discussion.—Certain antarctic amphipods exhibit morphological variability (Watling & Holman 1980, 1981; Barnard 1989). Previous descriptions of *Pseudiphimediella nodosa* show how the dorsal armament may vary. For example, Stebbing (1906) described one pair of dorsal teeth posteromarginally on pereonites 4 to 7: ". . . tubercular on segment 4, successively larger on following segments . . . ." Barnard (1932) described a specimen with pereon segments 1 to 6 being smooth. Schellenberg (1931) found a pair of short teeth on pereonite 5. The redescribed specimen bears a pair of very short blunt teeth on pereonite 5, and a pair of larger teeth on pereonite 6. Except for the Schellenberg reference it is probable that the other citations are based on erroneous identifications.

There are some differences in the maxillipedal palps of previously described specimens and the animal described herein. Barnard (1932) described the development of the maxillipedal palp: "2nd joint of palp slightly expanded distally, but scarcely produced." Watling & Holman (1980) found "that the maxillipedal palp articles 1 and 2 were not appreciably broadened . . . ," which resembles the conditions described by Barnard (1932). Contrary to these observations the redescribed specimen has broad palp articles 1 and 2 (article 2 medially produced) as in fig. 64 of Schellenberg's description and is densely covered with setae mediomarginally.

The shape of the telson may also vary. Barnard (1932) found that the telson of his specimen was apically slightly incised, but according to Schellenberg's figure the telson is apically truncate, whereas our specimen bears a rounded telson. The fourth maxillipedal palp article, observed by Watling and Holman, was not seen in this material, but it might easily be overlooked owing to the dense setation of article 3 (see also discussion of the description of *Pseudiphimediella glabra*).

Distribution.—Falkland Islands, Magellanic region, low tide to 150 m.

Pseudiphimediella glabra
(Schellenberg, 1931)
Figs. 5–10

Pariphimediella glabra Schellenberg, 1931: 121, fig. 65, pl. 1, fig. B.

Material.—2 females, 8.5 and 9 mm, Eltanin St. 974 (53°32'S, 64°57'W), 119–124 m, gear: 40'otter trawl, 12 Feb 1964.

Description.—Body (Fig. 6a, b): Slender; pereonite 1 longer than 2; pereonites 2 to 5 shortest; pereonite 6 with 2 teeth posteromarginally; pereonite 7 posteromarginally with 2 stout teeth dorsally and 2 shorter teeth laterally, posterolateral angles of pereonites 5 to 7 pointed. Metasomites 1 to 3 with similar arrangements of posteromarginal teeth as pereonite 7, but with keel-like tooth middorsally and flanked by dorsolateral teeth; keel-like tooth on metasomite 3 longest, with shorter dorsolateral teeth found in metasomites 1 and 2 not present; posteroventral angles acute, inconspicuous ridge on epimera 1 and 2. Urosomite 1 longest, with middorsal process, urosomite 2 shortest.

Head (Fig. 6a): Longer than pereonite 1, lateral cephalic lobe notched and ridged; rostrum relatively broad, acute, flexed.

Antenna 1 (Fig. 7a, b): Shorter than 2; peduncular article 1 stout, with 3 acute mediodistal processes, long plumose setae; article 3 shorter than 1 (58%), with acute process distally, article 3 shortest; accessory flagellum uniarticulate, inconspicuous (see detail of Fig. 7a); flagellar articles slender, every second article of second half with 1–2 aesthetascs and group of setae (as in detail of Fig. 6a).

Antenna 2 (Fig. 7c, e): Peduncular article

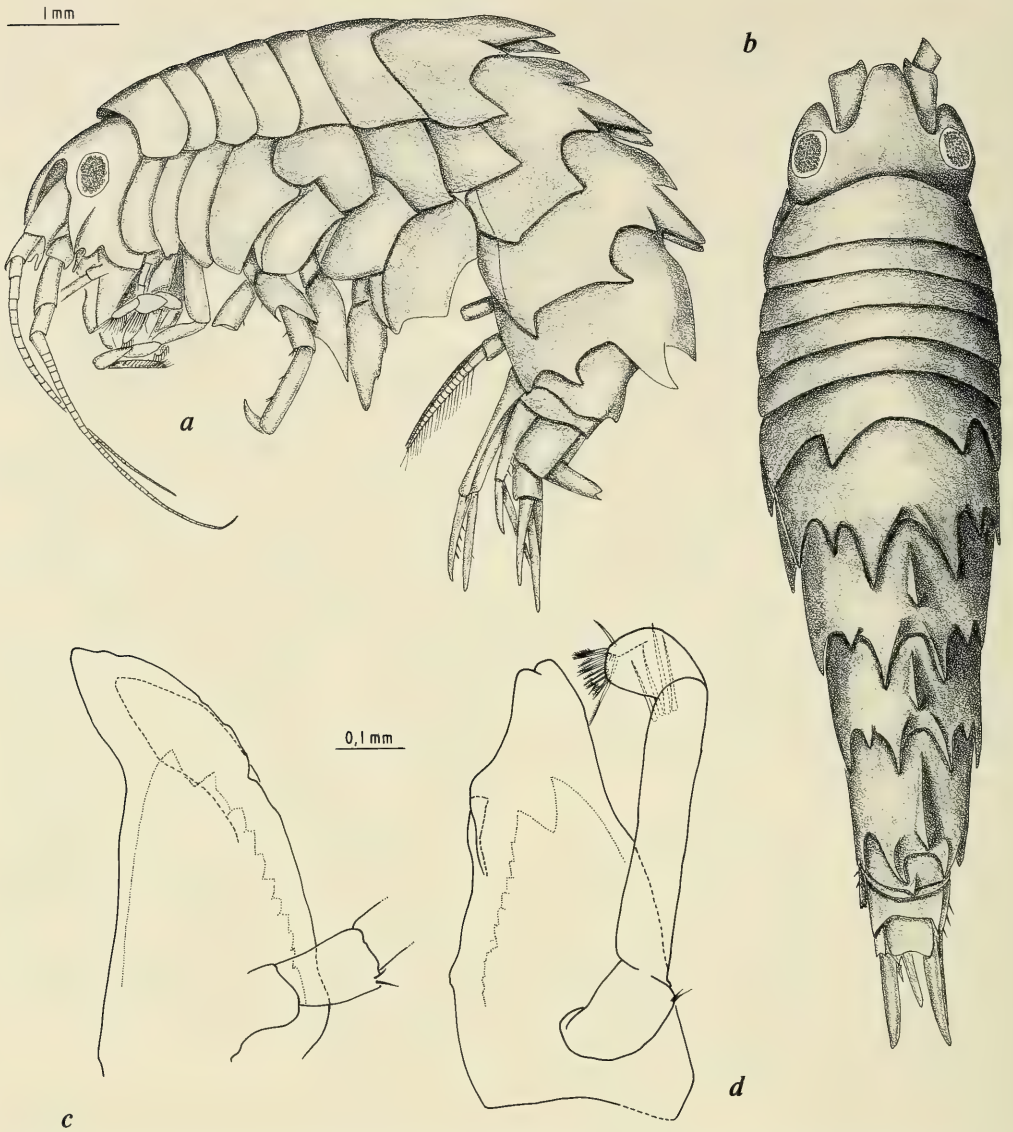


Fig. 6. a–d, *Pseudiphimediella glabra* female. a, left lateral view of habitus. b, dorsal view of habitus. c, left mandible. d, right mandible.

1 with long acute process; article 2 with 2 acute processes and short gland cone; article 3 short; article 4 slightly longer than article 5, with 2 processes distally, flagellum with 41 articles, each with group of short setae distally.

Labrum (Fig. 7f): Broad, rounded distally.

Mandible (Fig. 6c, d): Dentition of incisors abraded (but specimens are in premolt condition), preformed incisors and laciniae mobiles with sharp toothed cutting edges; lacinia mobiles on right mandible slender, on left mandible broad; palp 3-articulate, article 2 longest, distally with 4 long setae; article 3 strongly curved laterally with group of setae ventromarginally.

Lower lip (Fig. 7d): (Taken from other

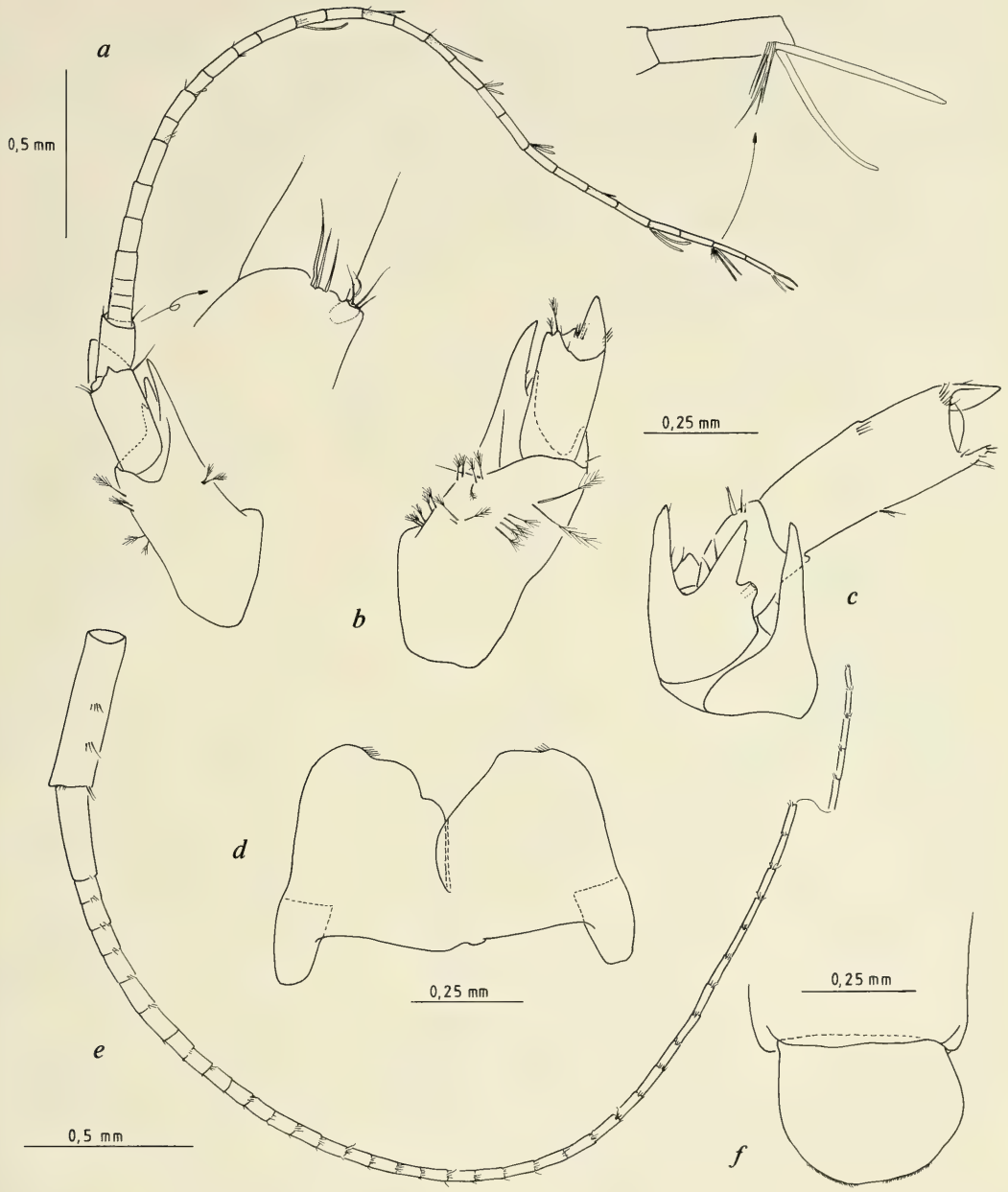


Fig. 7. a–f, *Pseudiphimediella glabra* female. a, antenna 1, details showing accessory flagellum and aesthetascs on flagellum. b, peduncular articles 1 and 2 of antenna 1. c, peduncular articles 1 to 4 of antenna 2. d, labium (lower lip), taken from other female. e, peduncular article 5 and flagellum of antenna 2. f, labrum (upper lip).

specimen) lobes broad, apices apically slightly sinuoid; mandibular projections short and rounded.

Maxilla 1 (Fig. 8b): Inner plate slightly shorter than outer plate, with 10 setae mediomarginally; outer plate with 11 spiniform setae, dentition abraded, preformed setae with sharp dentition; palp biarticulate, longer than outer plate with 7 setae distally.

Maxilla 2 (Fig. 8a): Inner plate wider than

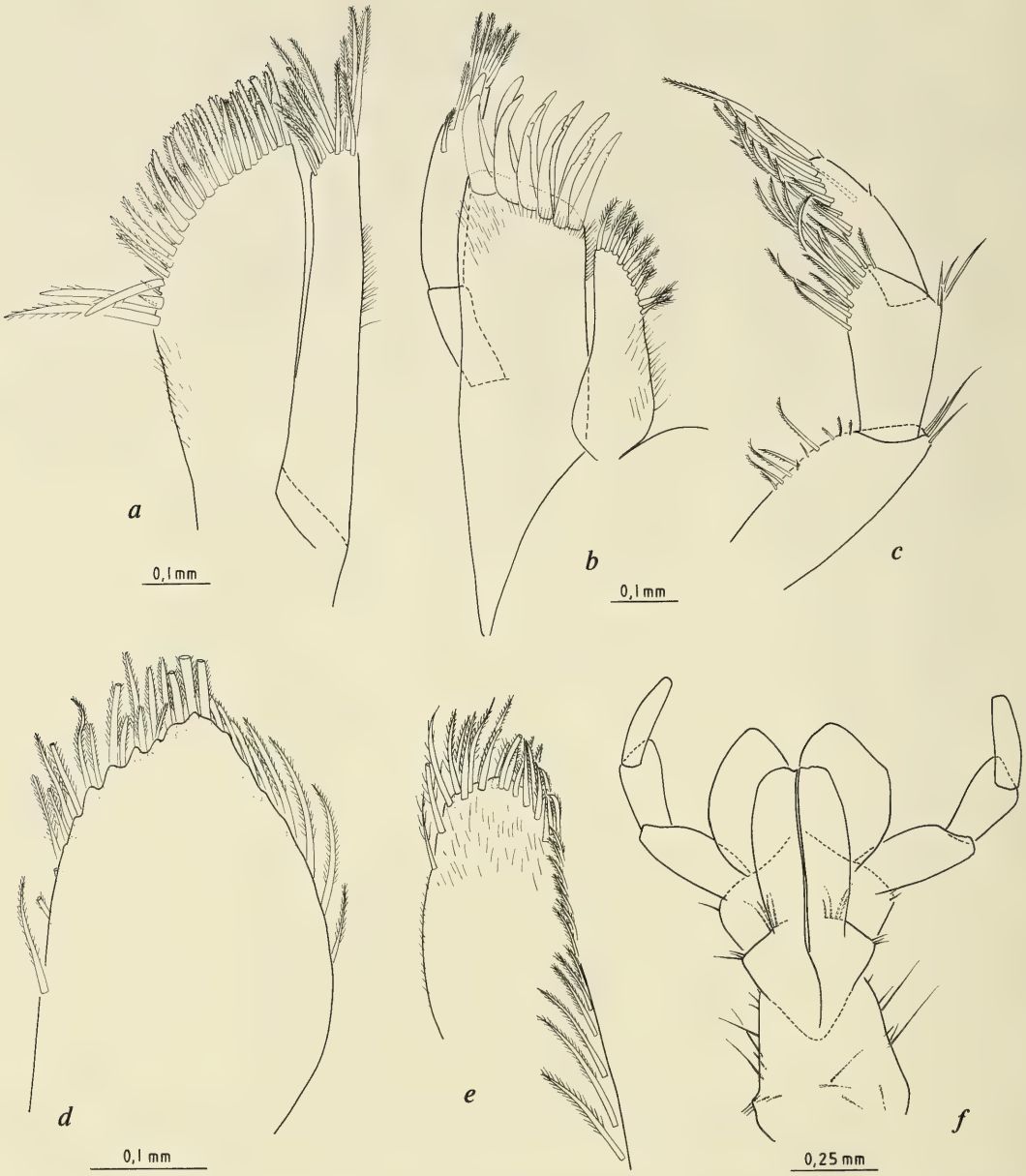


Fig. 8. a–f, *Pseudiphimediella glabra* female. a, maxilla 2. b, maxilla 1. c, maxillipedal palp, seen from ventral. d, outer plate of maxilliped, ventral view. e, inner plate of maxilliped seen from oral side. f, maxilliped seen from oral side, setae of plates and palps omitted.

outer plate, slightly expanded distally, with stout, relatively short, setulated setae distally; outer plate, slender, with longer setae distally.

Maxilliped (Fig. 8c–f): Inner plate shorter than outer (ca. 80%), with setulated setae mediomarginally and distally; outer plate broad with setulated setae marginally; palp

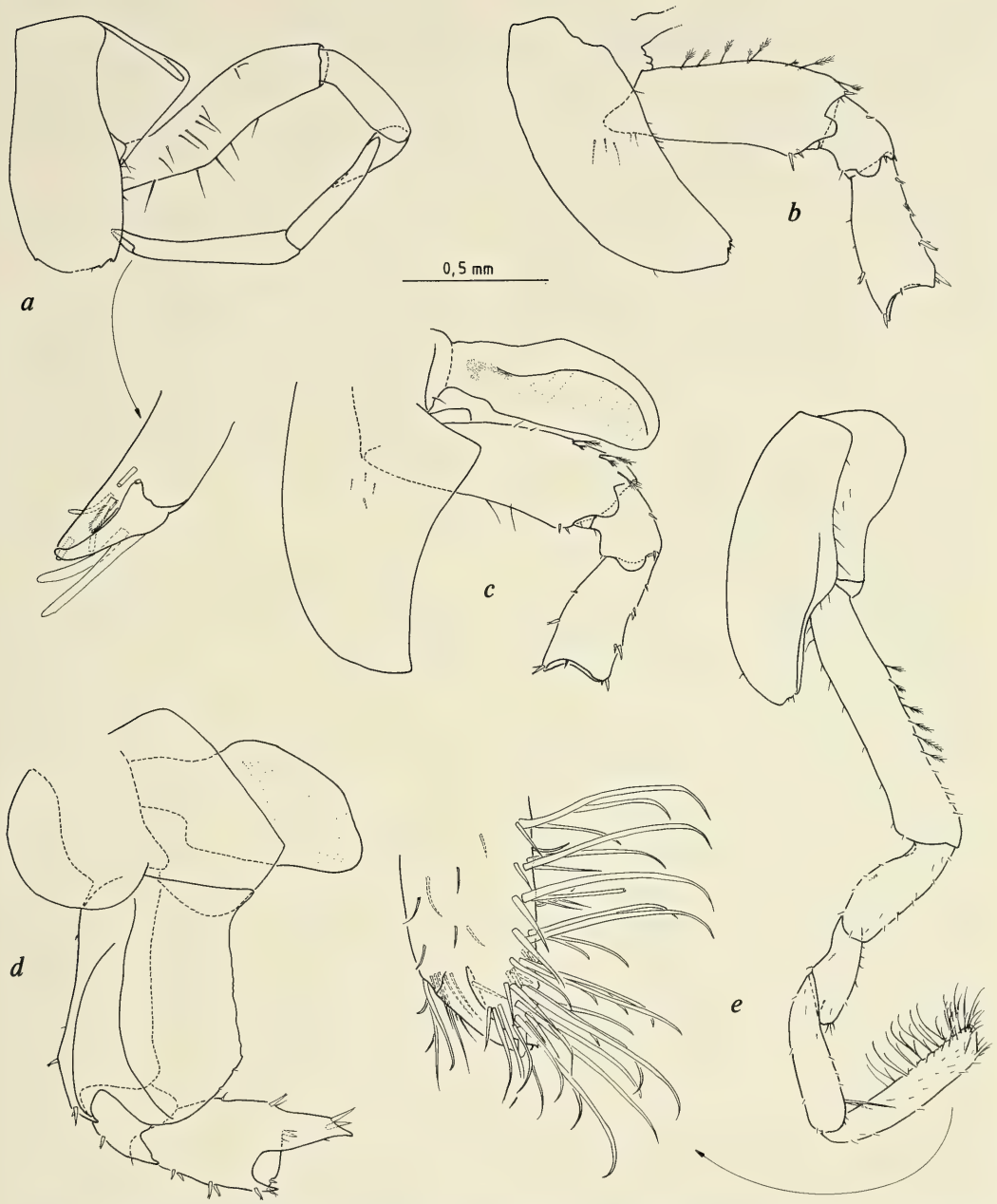


Fig. 9. a–e, *Pseudiphimediella glabra* female. a, gnathopod 1, detail showing chela. b, pereopod 3. c, pereopod 4. d, pereopod 5. e, gnathopod 2, detail showing chela.

4-articulate (fourth minute article may easily be overlooked using light-microscopy, see discussion), article 2 expanded distally, article 3 slender, setation as in Fig. 7c.

Gnathopod 1 (Fig. 9a): Coxa slightly expanded distally, truncate apically; basis elongated, shorter than coxa, slightly sinuoid; ischium elongate, just longer than

merus; carpus shorter than propodus (72%); propodus and dactylus forming chela (as in detail of Fig. 9a).

Gnathopod 2 (Fig. 9e): Coxa longer than coxa 1, tapering distally; basis elongate, subequal in length to coxa, longer than ischium and merus combined, with plumose setae posteromarginally; ischium longer than merus; carpus slightly shorter than propodus, with two long setae posterodistally; propodus and dactylus forming chela, propodus process wider than dactylus; setation of propodus as in detail of Fig. 9e.

Pereopod 3 (Fig. 9b): Coxa slightly longer than coxa 2, tapering distally; basis shorter than coxa, subequal in length to ischium and merus combined; plumose setae posteromarginally; ischium shorter than merus; merus slightly expanded distally, with spiniform setae marginally.

Pereopod 4 (Fig. 9c): Coxa longer than preceding coxae, with acute lobe posteromarginally, ventrally pointed; basis to merus as for pereopod 3.

Pereopod 5 (Fig. 9d): Coxa rounded anteriorly, subacute posterior lobe; basis broad with ridges; slightly excavate posteriorly, partly overlapping ischium, distally excavate; ischium short, pointed anteriorly; merus expanded distally, with acute process posterodistally, spiniform setae marginally.

Pereopod 6 (Fig. 10a): Coxa shorter than wide, pointed posteriorly and anteriorly; basis broader than basis 5, ridged, excavate ventrally and posteromarginally, spiniform setae anteromarginally; ischium and merus as for pereopod 5.

Pereopod 7 (Fig. 10b): Coxa shorter than long, pointed posteriorly; basis broader than basis of 5 and 6, ridged; 3 pointed processes posteromarginally, ventrally excavate, anteriorly with spiniform setae; ischium and merus as for pereopod 5.

Uropod 1 (Fig. 10d): Peduncle longer than rami, with spiniform setae marginally; rami slender, subequal in length, with spiniform setae marginally, slightly bifid apically.

Uropod 2 (Fig. 10e): Peduncle slightly shorter than inner ramus; outer ramus shorter than inner ramus (63%).

Uropod 3 (Fig. 10f, g): Peduncle short, stout, outer ramus as for uropods 1 and 2, inner ramus broader without spiniform setae.

Telson (Fig. 10c): Slightly longer than wide, notched posteriorly, some inconspicuous plumose setae on dorsal face.

Discussion.—The redescribed specimen resembles Schellenberg's (1931) description of this species very well. According to SEM examinations by Watling & Holman (1980) the maxillipedal palp is 4-articulate. The minute fourth article was not seen in the redescribed specimen using light microscopy.

Pseudiphimediella glabra is similar to *Pseudiphimediella nodosa*. They differ in the following: the habitus of *P. nodosa* is more robust, the dorsal teeth are broader and shorter compared to *P. glabra*. *P. glabra* bears a middorsal tooth on urosomite 1. The labrum of *P. nodosa* is incised, but truncate in *P. glabra*. The first peduncular article of antenna 1 of *P. nodosa* bears teeth of subequal length apically, but they are of different length in *P. glabra*. Article 2 of antenna 2 has short processes in *P. nodosa*, longer in *P. glabra*. The third article of the mandibular palp of *P. glabra* is strongly curved laterally, but normal in *P. nodosa*. The maxillulary palp is broader in *P. nodosa*. The inner plate of maxilla 2 is broad and expanded distally in *P. glabra* (normal in *P. nodosa*). Articles 1 and 2 of the maxillipedal palp are broadened and densely covered with setae in *P. nodosa* (possibly not always?). Gnathopod 1 of *P. nodosa* has a shorter merus, carpus and propodus than in *P. glabra*. Coxae 3 and 4 are wider in *P. nodosa*. The basis and ischium of pereopods 5 to 7 bear a conspicuous acute distal process in *P. nodosa* (short in *P. glabra*). The basis of pereopod 7 of *P. nodosa* is slightly excavate, forming two short processes, but

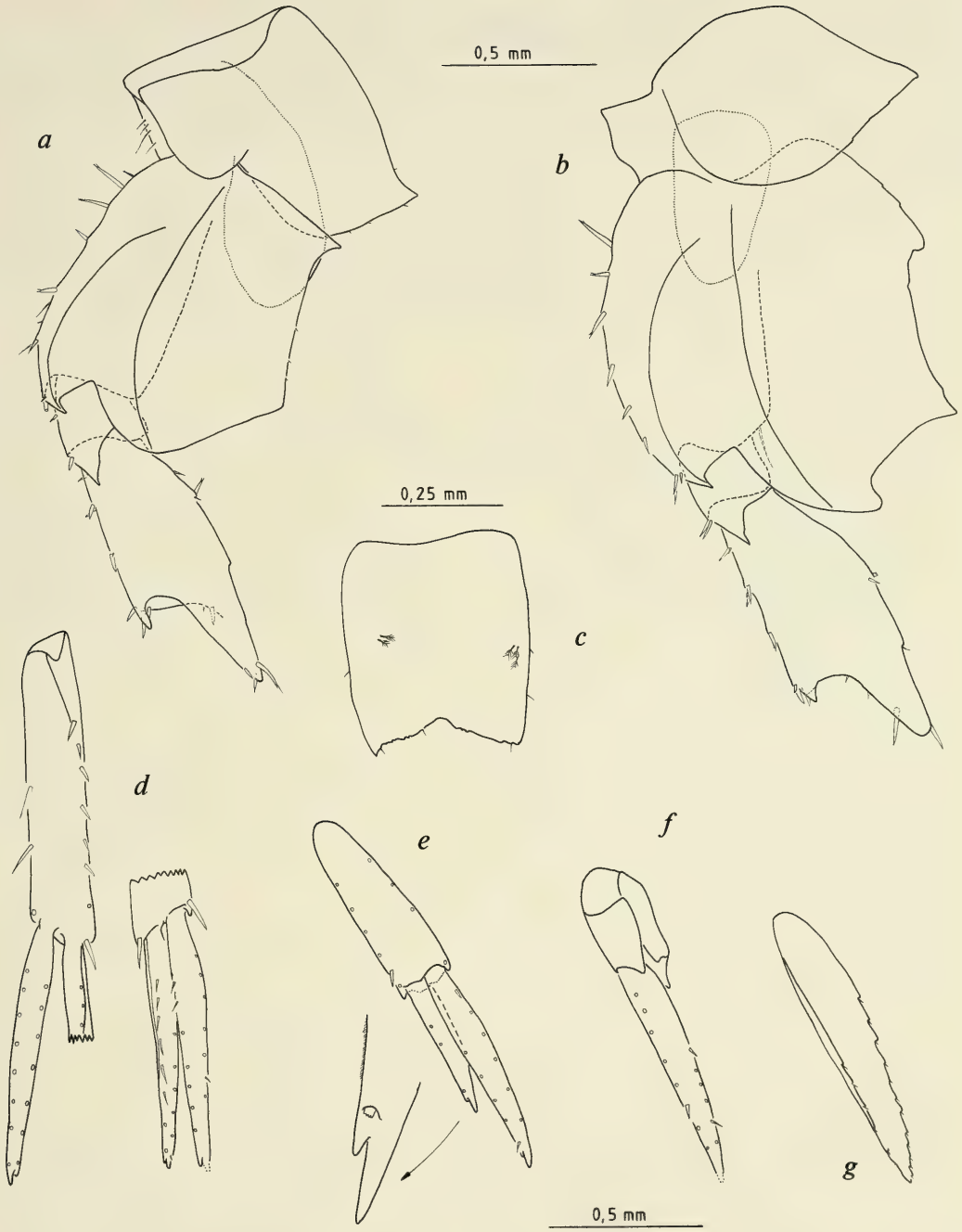


Fig. 10. a–g, *Pseudiphimediella glabra* female. a, pereopod 6, dotted line showing gill. b, pereopod 7, dotted line showing gill. c, telson. d, uropod 1. e, uropod 2, detail showing terminal cleft region. f, uropod 3, peduncle slightly damaged. g, inner ramus of uropod 3.

bi-excavate in *P. glabra* resulting in 3 processes. The telson of *P. nodosa* is rounded or truncate distally, but excavate in *P. glabra.*

Distribution.—Burdwood Bank, Falkland Islands, and many localities in the Magellanic region, 2–494 m.

Literature Cited

Barnard, J. L. 1989. Rectification of *Halirages regis* and *H. huxleyanus* (Crustacea: Amphipoda), from Marine Antarctica, with description of a new genus, *Austroregia.*—Proceedings of the Biological Society of Washington 102:701–715.

———, & C. M. Barnard. 1983. Freshwater Amphipoda of the World, I. Evolutionary patterns and II. Handbook and bibliography, xix and 830 pp., 50 figs., 7 graphs, 98 maps, 12 tables. Hayfield Associates, Mt. Vernon, Virginia.

Barnard, K. H. 1930. Amphipoda.—British Antarctic ("Terra Nova") expedition, 1910.—Natural History Reports, Zoology 8:307–454, 63 figs.

———. 1932. Amphipoda.—Discovery Reports 5:1–326, 174 figs., 1 pl.

Dana, J. D. 1853. Crustacea. Part II.—United States Exploring Expedition 14:689–1618, atlas of 96 pls.

Schellenberg, A. 1931. Gammariden und Caprelliden des Magellangebietes, Sudgeorgiens und der Westantarktis.—Further Zoological Results of the Swedish Antarctic Expedition 1901–1903 2(6):1–290, 1 pl., 136 figs.

Stebbing, T. R. R. 1906. Amphipoda I. Gammaridea.—Das Tierreich 21:1–806, 127 figs.

Watling, L., & H. Holman, 1980. New Amphipoda from the Southern Ocean, with partial revisions of the Acanthonotozomatidae and Paramphithoidae.—Proceedings of the Biological Society of Washington 93:609–654.

———, & ———. 1981. Additional acanthonotozomatid, paramphithoid, and stegocephalid Amphipoda from the Southern Ocean.—Proceedings of the Biological Society of Washington 94:181–227.

(COC) Fachbereich 7, Zoomorphologie, Universitat Oldenburg, Postfach 2503, D-2900, Oldenburg, F.R.G.; (JLB) NHB-163, Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 91–95

A NEW SPECIES OF CAPRELLID ASSOCIATED WITH HYDROIDS FROM SOUTHERN JAPAN (CRUSTACEA: AMPHIPODA: CAPRELLIDAE)

Masakazu Aoki

Abstract.—*Caprella glabra,* a new caprellid amphipod belonging to the *Caprella acutifrons* group, is described from Amakusa, southern Japan. The species is found in association with erect branching hydroids. Its unique pereopods 5–7 show a morphological adaptation to the hydroid substratum.

During ecological studies of a sublittoral community at Amakusa in western Kyushu, I found an unusual amphipod of the genus *Caprella* that occurs only on erect branching hydroids. This species belongs to the *Caprella acutifrons* group (see Mayer 1890, 1903) and displays some unique characters which appear to be morphological adaptations to life on the hydroid substratum. Consultation of the literature shows that it represents a new species, described below.

The type materials are deposited in the National Science Museum, Tokyo (NSMT) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Caprella glabra, new species
Figs. 1–3

Type material.—Holotype, ♂, 8.7 mm (NSMT-Cr 10174); allotype, ♀, 7.0 mm (NSMT-Cr 10175); paratypes, 10 ♂, 5 ♀ (NSMT-Cr 10176); paratypes, 10 ♂, 5 ♀ (USNM 239267), on *Thecocarpus niger* Nutting, *Sargassum patens* C. Agardh bed, 3 m, Tomioka, Amakusa Island, 32°31′N, 130°02′E, 9 Apr 1988, coll. M. Aoki; paratypes, 5 ♂, 5 ♀ (NSMT-Cr 10177), on *Aglaophenia whiteleggei* Bale, 4 m, Tomioka, Amakusa Island, 32°31′N, 130°02′E, 9 Apr 1988, coll. M. Aoki.

Diagnosis.—Body surface shiny, head with acute triangular projection directed straight forward, pereonite 3 with pair of sharp anterolateral projections, antenna 2 bearing sparse short setae, basis of gnathopod 2 longer than half of pereonite 2 in males, palmar margin of propodus of pereopods 5–7 defined by high triangular proximal projection bearing grasping spines.

Description.—Male: Pereonites 2, 4, 5 and 6 smooth. No pleura on pereonites 2–4. Pereonite 7 with small triangular process on posterodorsal margin. Pereonite 5 subequal in length to pereonites 6 and 7 combined. Maximum body length, 9.0 mm.

Antenna 1 shorter than half of body; peduncle barely as long as flagellum. Antenna 2 longer than peduncle of antenna 1; peduncle sparsely bearing short, simple and plumose setae; flagellum with hooks and simple setae.

Mouthparts typical of genus, lacina mobilis of right mandible 5-toothed.

Gnathopod 1 having palmar margin of propodus smooth and setose except for serrate proximal end with pair of grasping spines; grasping margin of dactylus serrate. Gnathopod 2 arising at midlength of pereonite 2 in adult; mesial and posterior sides of whole surface covered with fine granulations; palm of propodus barely setose, with 2 processes, proximal one spiniform, distal one triangular; basis ⅝ as long as propodus, more than half length of pereonite 2, with distolateral triangular process; dactylus apex diagonally truncate.

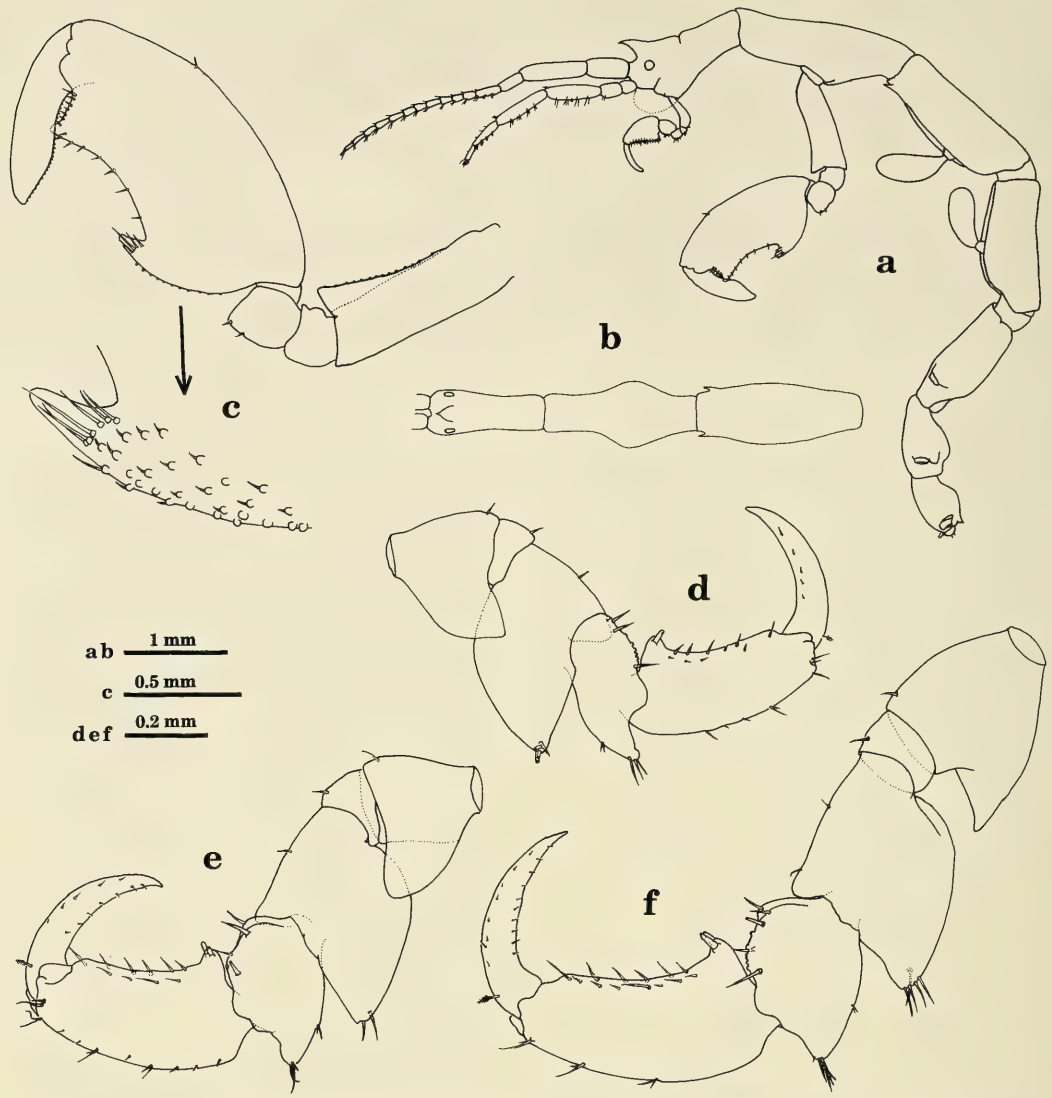


Fig. 1. *Caprella glabra,* new species, holotype male: a, lateral view; b, dorsal view of pereonites 1–3; c, left gnathopod 2; d, right pereopod 5; e, left pereopod 6; f, left pereopod 7.

Gills elliptical.

Pereopods 5, 6 and 7 increasing in length posteriorly; grasping margins of dactylus and propodus carinate and smooth, with few short setae; palm of propodus slightly concave, with high triangular proximal projection; margins of basis and merus posterolaterally expanded to form triangular plates with smooth margins. Pereopod 5 with proximal grasping spine on palmar lateral margin; pereopods 6 and 7 with paired grasping spines.

Abdomen typical of genus, with pair of unsegmented appendages and pair of setose lobes; penes medial.

Female: Maximum body length, 7.0 mm. Gnathopod 2 arising from anterior of pereonite 2, and surface not granular; palm of

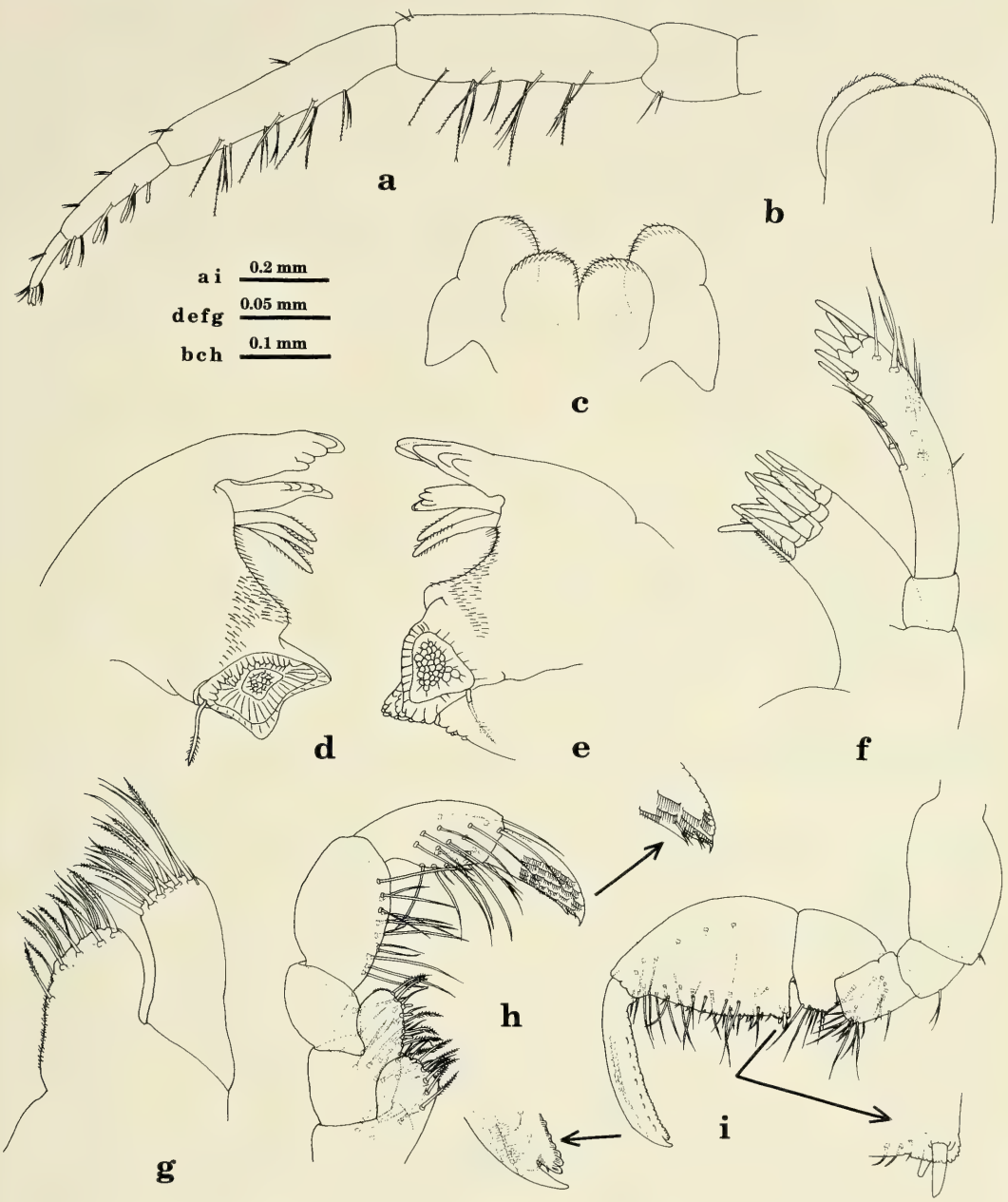


Fig. 2. *Caprella glabra,* new species, holotype male: a, left antenna 2; b, upper lip; c, lower lip; d, left mandible; e, right mandible; f, maxilla 1; g, maxilla 2; h, maxilliped; i, gnathopod 1.

propodus with 3 processes, proximal one triangular with single grasping spine mesial to margin, medial one spiniform, occasionally triangular, distal one spiniform.

Etymology.—From the Latin *glaber* (smooth or hairless) referring to the barely setose, smooth body.

Systematics.—*Caprella glabra* apparent-

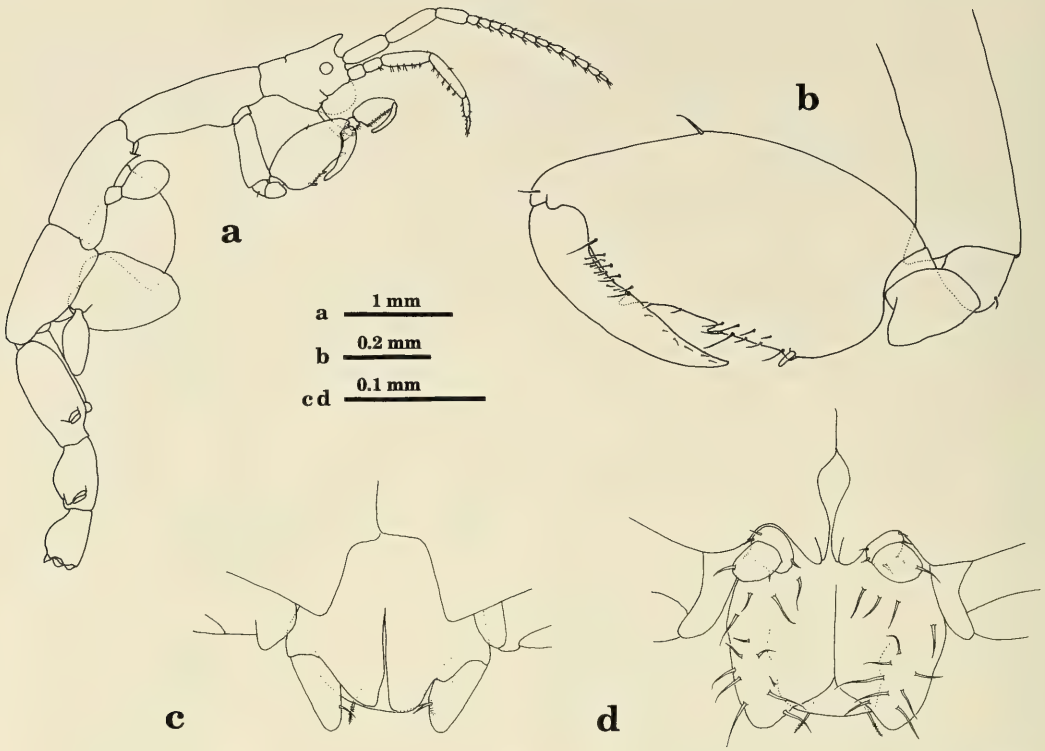


Fig. 3. *Caprella glabra,* new species: a, b, allotype female; c, paratype female (NSMT-Cr 10176D); d, paratype male (NSMT-Cr 10176B). a, lateral view; b, right gnathopod 2; c, female abdomen; d, male abdomen.

ly belongs to the *C. acutifrons* group (Mayer 1890, 1903), which is characterized by an anteriorly directed triangular rostrum-like projection on the head. The taxonomic status of the species within the *C. acutifrons* group has been discussed (McCain 1968, Laubitz 1972). The body that is slender, smooth, shiny and barely setose, the pereonites 2–4 that have no distinct pleura, and the gnathopod 2 that has the palm barely setose with a distal triangular process and a large proximal "poison tooth" (McCain 1968), links the new species strongly to the form *natalensis,* one of the 20 varieties (forms) proposed by Mayer (1890, 1903). The form *natalensis* is given a specific status as *Caprella natalensis* by Laubitz (1972). However, the pair of sharp anterolateral processes on the pereonite 3, the basis of gnathopod 2 which is proportionally longer than in other forms, and the sparsely setose antenna 2 differentiate *C. glabra* from the form *natalensis* as well as from other forms in the group.

Ecology.—*Caprella penantis,* a close relative of *Caprella glabra,* is taken on many substrata, e.g., red and brown algae, seagrasses, sponges, hydroids, bryozoans, gorgonians, etc. (see McCain 1968, Bynum 1980). On the other hand, *C. glabra* was collected only from *Thecocarpus niger* and *Aglaophenia whiteleggei,* erect branching hydroids (identified by I. Isasi). Some caprellids with specific habitat preferences exhibit morphological adaptations to their substrata in their pereopods (Caine 1978, Vader 1983, Aoki & Kikuchi 1990). There are various modes by which caprellids hold the substratum: holding thick rod between two pereopods, encircling middle-sized rod with the propodus and dactylus of a pereopod, grasping thin rod with tightly closed

propodus and dactylus, clutching flat surface with widely opened propodus and dactylus, and anchoring dactylus in soft substratum (Wetzel 1932, Caine 1978). The characteristic pereopods 5–7 of *C. glabra* appear to be well adapted to grasp thin branches of hydroids. The high proximal palmar defining projection of the species changes the shape of the foot by increasing the concavity of the palmar surface, which presumably enhances the grasping capability.

Most of the known species of *Caprella* have the antenna 2 with dense swimming setae, and the species in the genus which have been studied feed primarily by filtering or by scraping (Caine 1974, 1977, 1979). The sparse short swimming setae of *C. glabra* suggest that filtering is unlikely and the primary mode of feeding must be different from that of most species in the genus *Caprella.*

Acknowledgments

I thank Dr. T. Kikuchi of the Amakusa Marine Biological Laboratory, Kyushu University, for his continuous guidance and support for this study. I am indebted to Dr. K. Baba of Kumamoto University and Dr. D. R. Laubitz of the National Museum of Canada for their critical reading of a draft of the manuscript. I acknowledge Mr. I. Isasi of the University of the Basque Country, Spain, for identification of the hydroids. My colleagues at the Amakusa Marine Biological Laboratory are also thanked for their invaluable advice and encouragement. This is contribution no. 348 from the Amakusa Marine Biological Laboratory, Kyushu University.

Literature Cited

Aoki, M., & T. Kikuchi. 1990. Habitat adaptations of caprellid amphipods and the importance of epiphytic secondary habitats in a *Sargassum patens* bed in Amakusa, southern Japan.—Publications from the Amakusa Marine Biological Laboratory, Kyushu University 10:123–133.

Bynum, K. H. 1980. Multivariate assessment of morphological variation in *Caprella penantis* Leach, 1814 (Amphipoda: Caprellidae).—Estuarine and Coastal Marine Science 10:225–237.

Caine, E. A. 1974. Comparative functional morphology of feeding in three species of caprellids (Crustacea, Amphipoda) from the northwestern Florida Gulf Coast.—Journal of Experimental Marine Biology and Ecology 15:81–96.

———. 1977. Feeding mechanisms and possible resource partitioning of the Caprellidae (Crustacea: Amphipoda) from Puget Sound, USA.—Marine Biology (Berlin) 42:331–336.

———. 1978. Habitat adaptations of North American caprellid Amphipoda (Crustacea).—Biological Bulletin (Woods Hole) 155:288–296.

———. 1979. Functions of swimming setae within caprellid amphipods (Crustacea).—Biological Bulletin (Woods Hole) 156:169–178.

Laubitz, D. R. 1972. The Caprellidae (Crustacea, Amphipoda) of Atlantic and Arctic Canada.—National Museum of Natural Sciences (Ottawa), Publications in Biological Oceanography 4:1–82.

Mayer, P. 1890. Die Caprelliden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Eine Monographie. Nachtrag zur Monographie derselben.—Fauna und Flora des Golfes von Neapel 17:i–vii + 1–157.

———. 1903. Die Caprellidae der Siboga-Expedition.—Siboga-Expeditie 34:1–160.

McCain, J. C. 1968. The Caprellidae (Crustacea: Amphipoda) of the western North Atlantic.—Bulletin of the United States National Museum 278: i–vi + 1–147.

Vader, W. 1983. Prehensile pereopods in gammaridean Amphipoda.—Sarsia 68:139–148.

Wetzel, A. 1932. Studien über die Biologie der Caprelliden. I. Bewegung, Nahrungserwerb, Aufenthaltsort.—Zeitschrift für Wissenschaftliche Zoologie 141:347–398.

Amakusa Marine Biological Laboratory, Kyushu University, Tomioka, Reihoku, Amakusa, Kumamoto 863-25, Japan.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 96–100

PHOTIS TRAPHERUS, A NEW ELEPHANTINE SPECIES FROM THE CARIBBEAN SEA (CRUSTACEA: AMPHIPODA)

James Darwin Thomas and J. L. Barnard

Abstract.—*Photis trapherus* differs from its Californian counterpart, *P. elephantis,* in characters of male pereopod 6: the smallness of the posteroventral tooth on article 2, the longer article 4 with separated posterior keel and no significant posteroventral lobe, the relatively thinner article 2; the lack of distal expansion on article 4 of pereopod 7; the distinct concavity and defining tooth on the palms of gnathopods 1–2.

Photis trapherus, new species
Figs. 1–3

Etymology.—Gr., trapheros, stout.

Diagnosis.—Male eyes not enlarged; coxae 1–2 not shortened; coxa 3 not much wider than coxa 4; gnathopods 1–2 feeble, with distinctly concave palm and defining tooth, article 2 not produced anterodistally, stridulation ridges absent everywhere; pereopod 6: posteroventral tooth on article 2 very small, article 4 extremely elongate, with separated posterior keel and no significant posteroventral lobe, article 2 much thinner than article 4; distal expansion on article 4 of pereopod 7 absent.

Female.—Like typical male but pereopod 6 of ordinary photis form. Gnathopods like typical male as represented by male "a."

Male "k."—Gnathopod 2 slightly enlarged, propodus broader than in typical male as represented by holotype, palm below main notch much broader, with distinct tooth between main notch and finger hinge, dactyl more slender, main inner spine relatively smaller than in typical male.

Holotype.—USNM 242013, male "a" 4.88 mm.

Type locality.—Pte. Guignard, Dominica, 7 m, coarse quartz sand with large amounts of dark mineral grains and unicellular algal strands, 19 May 1987, coll. J. D. Thomas.

Material.—Paratypes, type-locality only, ovigerous female "c" 2.50 mm, male "d" 3.58 mm and 5 other specimens. Jioquito Bay, Dominican Republic, 19°53.2′N, 71°38.5′W, 2 m, muddy sand in mangroves, 7 Nov 1980, coll. R. P. Higgins and B. W. Pollock, male "j" 2.55 mm, male "k" 2.53 mm and 50 + other specimens. Walker Cay, Turks and Caicos Islands, benthic washings, 1 m, 14 April 1988, coll. R. Heard, 60 specimens. Discovery Bay, Jamaica, 7 Sep 1986, algal covered rubble on fore-reef, 3–4 m, JDT-JAM 2A, J. D. Thomas, collector, 13 specimens. Key Largo, Florida, canal, 3 m, 7 Sep 1987, station LAC, 1 specimen.

Remarks.—As demonstrated with silver nitrate stain, penial processes are present on both hypermales (with elephantine pereopod 6) and normal or younger males that resemble females. Males with pereopod 6 fully developed have gnathopod 2 like females and do not lose the penial processes. It appears, therefore, that the previous report (Barnard, 1962) suggesting the elephantine condition of the pereopods might result from neutering by a parasite is unwarranted. As described for male "k" above, the "extremely" terminal male has a better developed gnathopod 2 than other males.

Relationship.—Differing from the similar *Photis elephantis* J. L. Barnard, 1962, from California, in characters of male pereopod

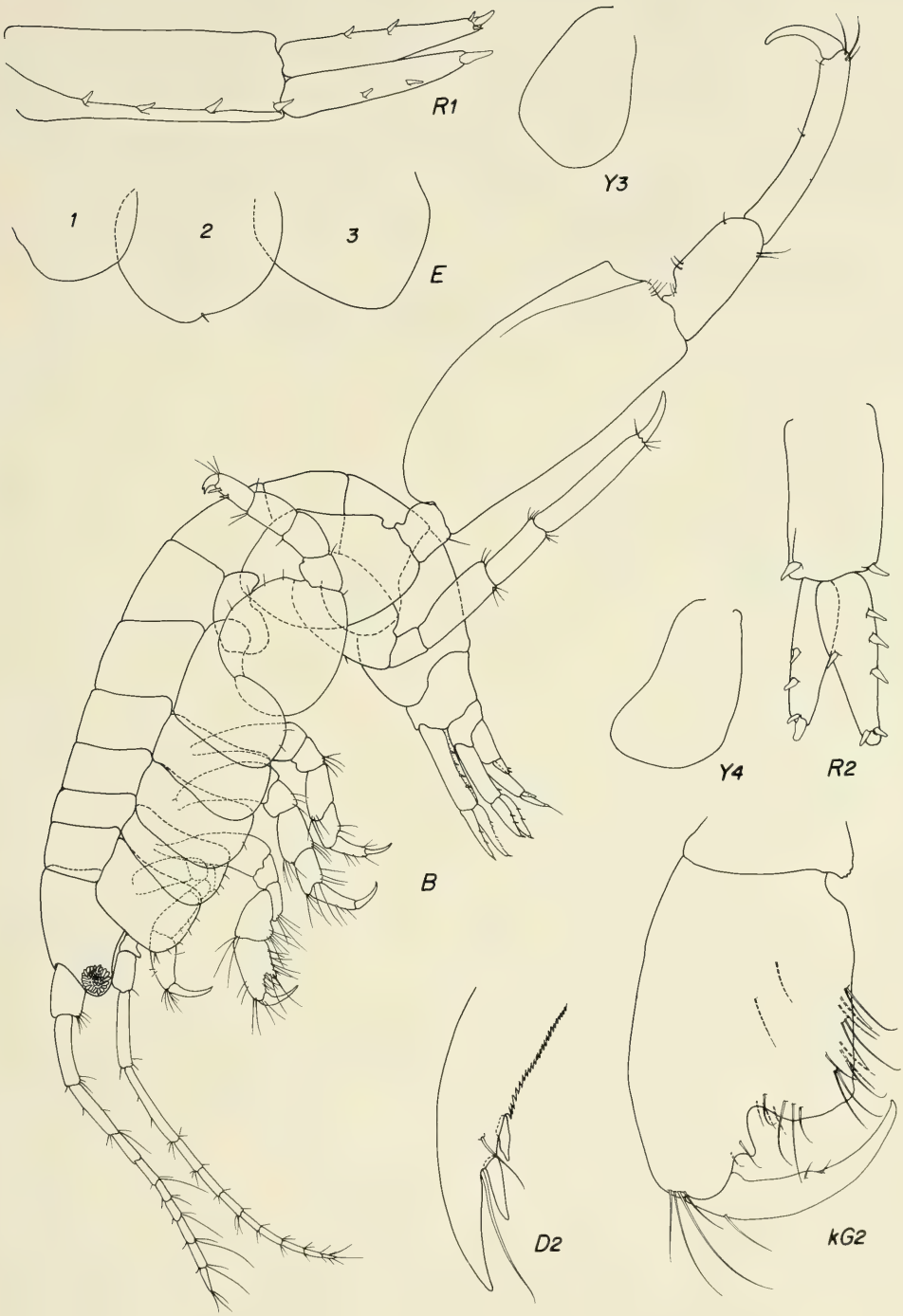


Fig. 1. *Photis trapherus*, new species, figures lacking letter to left of labels = holotype male "a" 4.88 mm; k = male "k" 2.53 mm. Capital letters in figures refer to parts; lower case letters to left of capital letters refer to specimens and to the right refer to adjectives as described below: B, body; C, coxa; D, dactyl; E, epimeron(a); G, gnathopod; L, labium; M, mandible; N, right molar; P, pereopod; Q, left lacinia mobilis; R, uropod; S, maxilliped; T, telson; U, upper lip; X, maxilla; r, right; t, left.

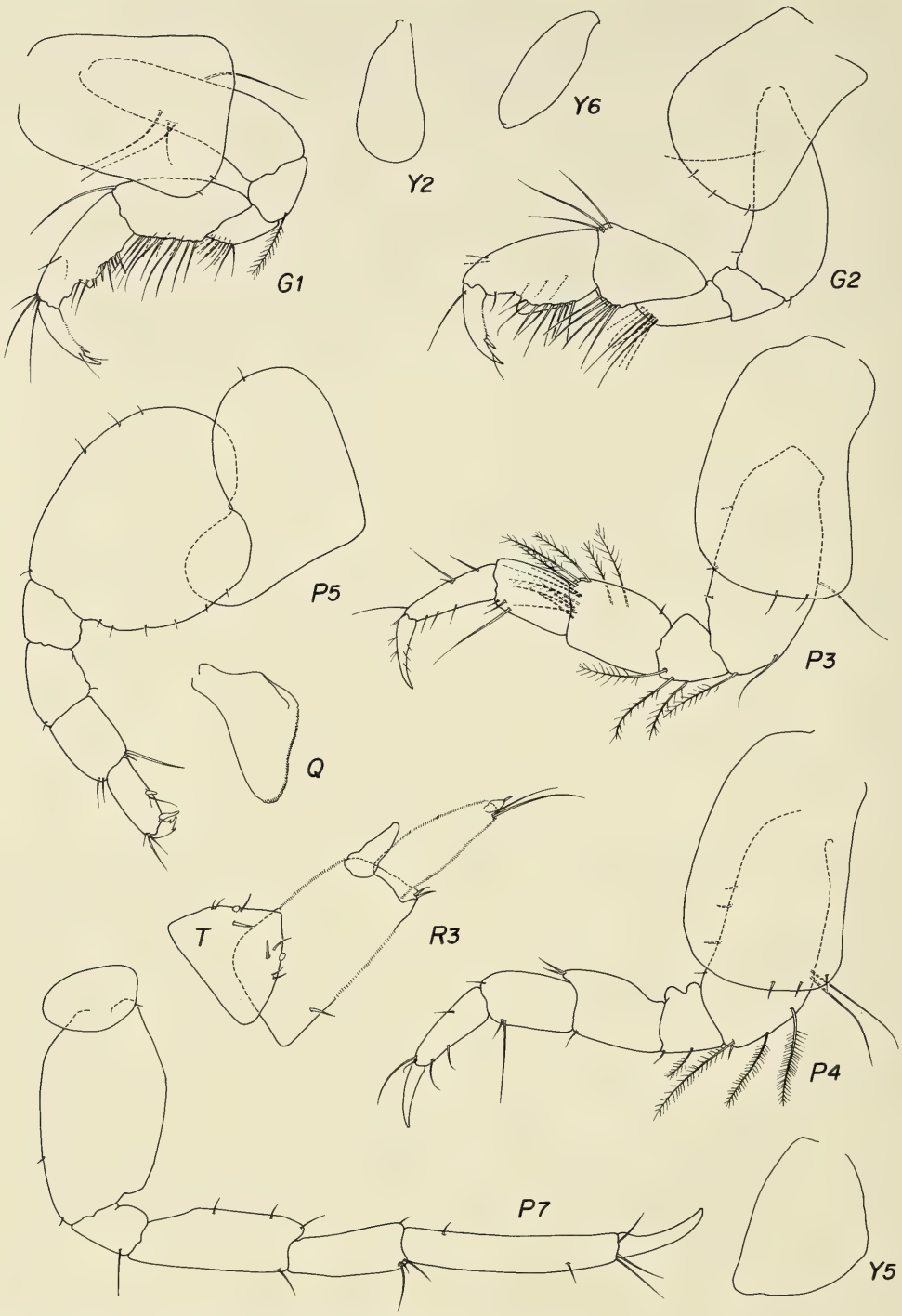


Fig. 2. *Photis trapherus,* new species, holotype male "a" 4.88 mm.

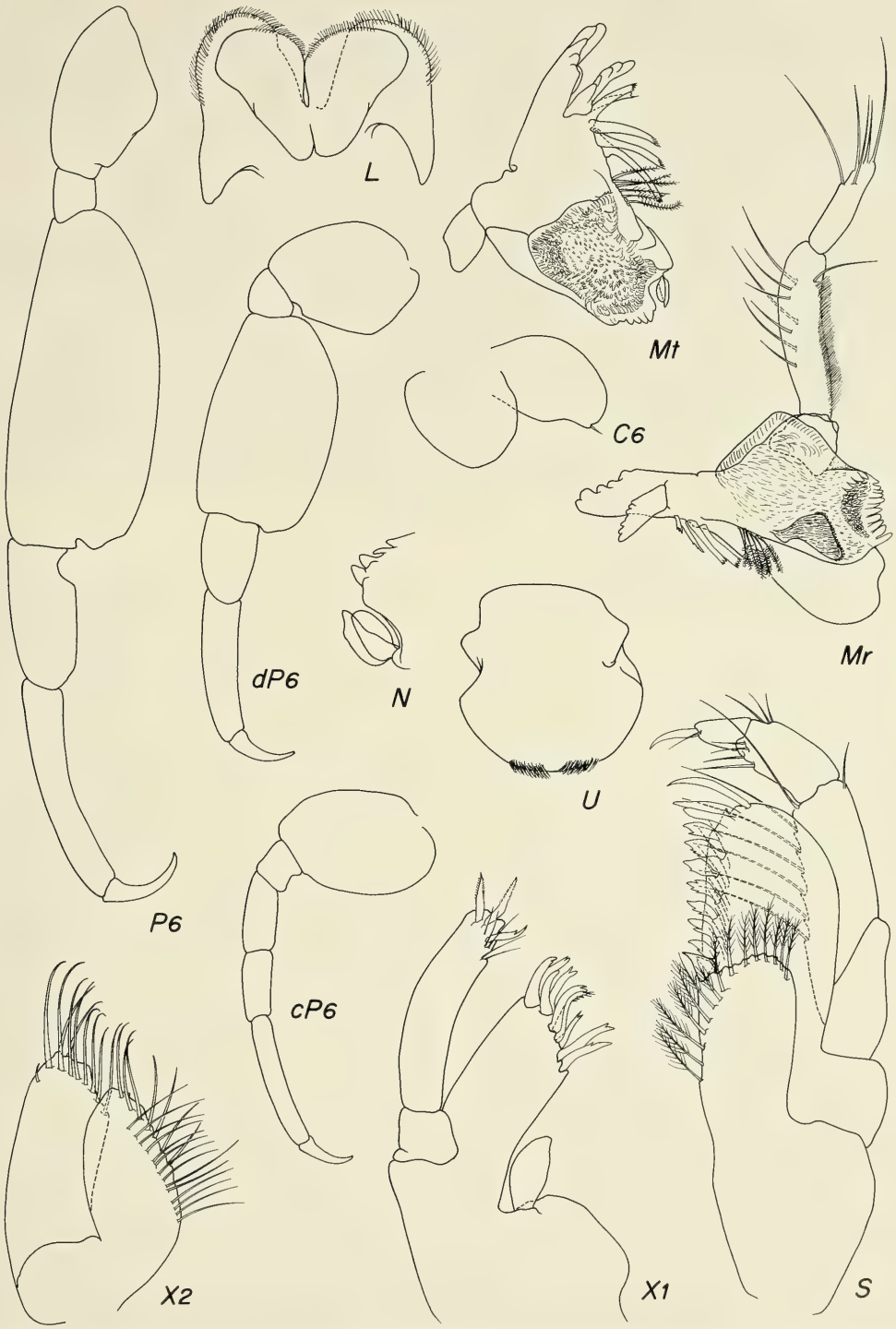


Fig. 3. *Photis trapherus,* new species, figures lacking letter to left of labels = holotype male "a" 4.88 mm; c = female "c" 2.50 mm; d = male "d" 3.58 mm.

6: the smallness of the posteroventral tooth on article 2, the longer article 4 with separated posterior keel and no significant posteroventral lobe, the relatively thinner article 2; the lack of distal expansion on article 4 of pereopod 7; the distinct concavity and defining tooth on the palms of gnathopods 1–2.

Distribution.—Dominica (Lesser Antilles); Dominican Republic (Greater Antilles); Turks and Caicos Islands (near Bahamas); Jamaica; Key Largo, Florida; 1–7m.

Acknowledgments

We thank R. P. Higgins and R. W. Heard for collections of the material. The first author was supported by NSF Grant BSR8515186. We thank the CCRE committee and Dr. K. Ruetzler, of Smithsonian Institution, for funds to travel to Dominica. This is Contribution No. 279 of the CCRE committee of the National Museum of Natural History.

Literature Cited

Barnard, J. L. 1962. Benthic marine Amphipoda of southern California: families Aoridae, Photidae, Ischyroceridae, Corophiidae, Podoceridae.—Pacific Naturalist 3:1–72, 32 figs.

(JDT) Reef Foundation, P.O. Box 569, Big Pine Key, Florida 33043; (JLB) NHB-163, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 101–137

COPEPODA ASSOCIATED WITH THE SCLERACTINIAN CORAL GENUS *MONTIPORA* IN THE INDO-PACIFIC

Arthur G. Humes

Abstract.—Six new species and 2 new genera, *Hetairosyna* and *Tychomyzon,* are added to the 14 species of copepods already known to be associated with various species of the hard coral genus *Montipora* in the Indo-Pacific. The new species include the cyclopoid *Euryte bellatula,* the asterocherid siphonostomatoids *Hetairosyna terpna, Hetairosyna laciniata, Hetairosyna sororia,* and *Tychomyzon petalum,* and the lichomolgid poecilostomatoid *Haplomolgus incolumis.* New host and locality records for the lichomolgids *Haplomolgus montiporae* Humes & Ho, 1968, and *Odontomolgus forhani* Humes, 1978, are given. A list of all copepods known to be associated with *Montipora* is provided.

The acroporid scleractinian coral genus *Montipora* is widespread in shallow waters of the tropical Indo-Pacific Ocean, from Madagascar and the Red Sea to Japan, Australia, Hawaii, and the Marquesas (Veron 1986). Two hundred and eleven nominal species are known, but the number of true species is unknown, with 38 true species reported from Australia (Veron 1986). Copepods are associated with species of *Montipora* in Madagascar (Humes & Ho 1968a, 1968b; Humes & Dojiri 1982, 1983), Mauritius (Stock 1966); India (Sebastian & Pillai 1974); the Moluccas (Humes 1978, Humes & Dojiri 1982); northeastern Australia (Humes 1978, 1984; Humes & Dojiri 1982), New Caledonia (Humes 1978, Humes & Dojiri 1982); and Hawaii (Humes 1984).

In this work a new species of copepod is reported from *Montipora* at Enewetak Atoll in the Marshall Islands. Other new species, representing two new genera, are described from Madagascar, the Moluccas, northeastern Australia, and New Caledonia. New host and distribution records are recorded for certain species. The number of species of copepods living with members of this large coral genus is now increased from 14 to 20. A list of the corals and their associated copepods is provided.

Materials and Methods

The collection of the copepods covered a span of 19 years, from 1963–1982. Since the colonies of *Montipora* were often too large to be collected whole, fragments were isolated in plastic bags in sea water. In the laboratory, the corals were soaked for several hours in sea water with sufficient ethyl alcohol added to make a solution of approximately 5%. After rinsing the corals, the water was passed through a fine net (120 holes per 2.5 cm, each hole approximately 120 μm square). The copepods were then removed from the sediment retained in the net.

The copepods were measured and dissected in lactic acid, using the wooden slide technique described by Humes & Gooding (1964). All figures were drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn. The body length does not include the setae on the caudal rami. The lengths of the segments of the first an-

tennae were measured along their posterior nonsetiferous margins. In the formulas for the armature of legs 1–4 the Roman numerals indicate spines, the Arabic numerals represent setae.

The abbreviations used are: R = rostrum, A_1 = first antenna, A_2 = second antenna, S = siphon, MD = mandible, P = paragnath, MX_1 = first maxilla, MX_2 = second maxilla, MXPD = maxilliped, and P_1 = leg 1.

Order Cyclopoida Burmeister, 1834
Family Cyclopidae Dana, 1853
Genus *Euryte* Philippi, 1843

Euryte bellatula, new species
Figs. 1, 2, 3

Type material.—4 ♀, 2 ♂ from *Montipora compressa* (Esper), in 2 m, Natsepa, Ambon, Moluccas, 03°37′05″S, 128°17′00″E, 28 May 1975. Holotype ♀ (USNM 254456), allotype (USNM 254457), and 3 paratypes (2 ♀, 1 ♂) (USNM 254458) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. One female paratype (dissected) in the collection of the author.

Other specimens.—6 ♀ from *Montipora lobulata* Bernard, in 0.5 m, Rocher à la Voile, Noumea, New Caledonia, 22°18′24″S, 166°25′50″E, 17 Jun 1971 (1 ♀ dissected); 4 ♀, 1 ♂ from *Montipora caliculata* (Dana), in 1.5 m, Ricaudy Reef, near Noumea, 22°19′05″S, 166°26′28″E, 25 Jun 1971; 1 ♀ from *Montipora ramosa* Bernard, in 2 m, north of Isle Maître, near Noumea, 22°19′30″S, 166°24′35″E, 13 Jul 1971; 1 ♀, 1 ♂ from *Montipora prolifera* Brueggemann, in 3 m, southern shore of Goenoeng Api, Banda Islands, Moluccas, 04°32′05″S, 129°52′30″E, 26 Apr 1975 (♂ dissected); 2 ♀ from *Montipora verrilli* Vaughan, in 3 m, Mermaid Cove, Lizard Island, northeastern Australia, 14°39′50″S, 145°27′00″E, 27 Oct 1982.

Female.—Body (Fig. 1a) slender and elongate. Length 0.83 mm (0.80–0.87 mm) and greatest width 0.31 mm (0.30–0.32 mm), based on 10 specimens. Greatest dorsoventral thickness 0.22 mm. Epimera of segment bearing leg 1 pointed posteriorly, those of segments bearing legs 2 and 3 subtruncate, and those of segment bearing leg 4 rounded. Ratio of length to width of prosome 1.52:1. Ratio of length of prosome to that of urosome 1.25:1.

Segment bearing leg 5 (Fig. 1b) 47 × 161 μm in dorsal view, pointed posterolaterally. Genital segment in dorsal view (Fig. 1c) elongate, 107 μm long, 86 μm in greatest width, and 58 μm in least width. Lateral spiniform process (Fig. 1c, d) present on both sides almost midway on segment. Genital areas located dorsolaterally near widest part of segment (Fig. 1c), both areas connected by duct to single midventral pore (Fig. 1d, e). Each area with 2 small hyaline setae approximately 20 μm (Fig. 1d). Three postgenital segments from anterior to posterior 39 × 55, 31 × 52, and 44 × 47 μm.

Caudal ramus (Fig. 1f) elongate, unornamented, 73 × 18 μm, ratio 4.06:1. Outer lateral seta short, 15 μm, dorsal seta 28 μm, both smooth. Outermost terminal seta 52 μm, innermost terminal seta 96 μm, and 2 long median terminal setae 210 μm (outer) and 340 μm (inner), all with lateral setules.

Body surface without visible ornamentation.

Egg sac (seen on only 1 female) (Fig. 1g) containing 2 eggs 125 × 125 μm and 146 × 120 μm.

Rostrum (Fig. 2a, b) linguiform. First antenna (Fig. 2c) 273 μm long, 21-segmented. Lengths of segments: 28 (53 μm along anterior margin), 20, 11, 7.5, 6.5, 6.5, 6.5, 6.5, 11, 12, 13, 10, 9, 9, 11, 9, 9, 9, 12, 12, and 20 μm, respectively. Armature: 8, 3, 2, 2, 2, 2, 2, 2, 2, 1, 1, 1, 1, 0, 1, 1, 1, 1, 2, 2, and 8. All setae smooth.

Second antenna (Fig. 2d) 4-segmented, 160 μm long without setae. Armature: 3, 1, 5, and 6, with 4 terminal setae slightly geniculate. Fourth segment with row of inner marginal setules.

Labrum (Fig. 2a, e) with median denticles

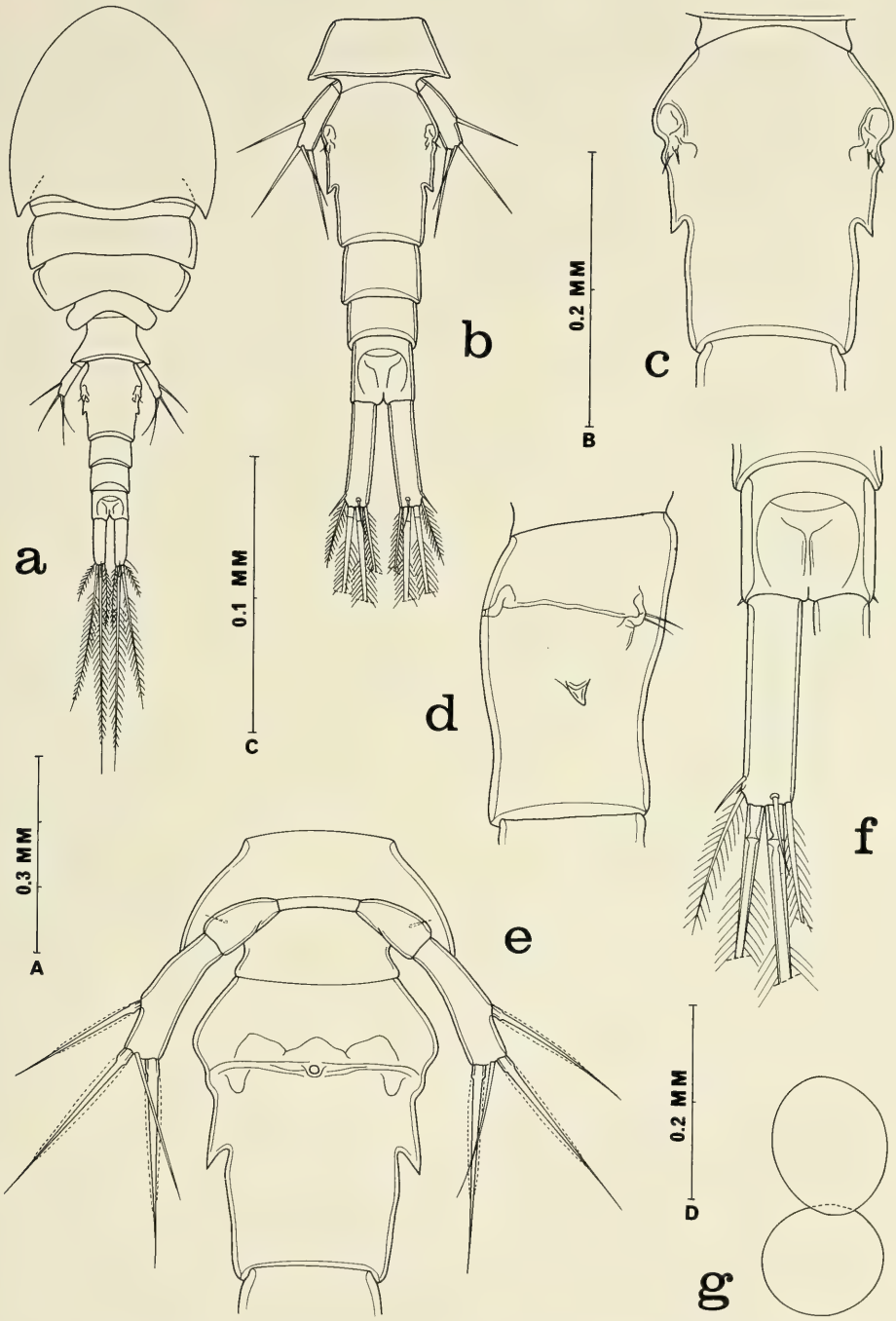


Fig. 1. *Euryte bellatula,* female. a, Dorsal (scale A); b, Urosome, dorsal (B); c, Genital segment, dorsal (C); d, Genital segment, lateral (C); e, Segment bearing leg 5 and genital segment, ventral (C); f, Anal segment and caudal ramus, dorsal (C); g, Egg sac, ventral (D).

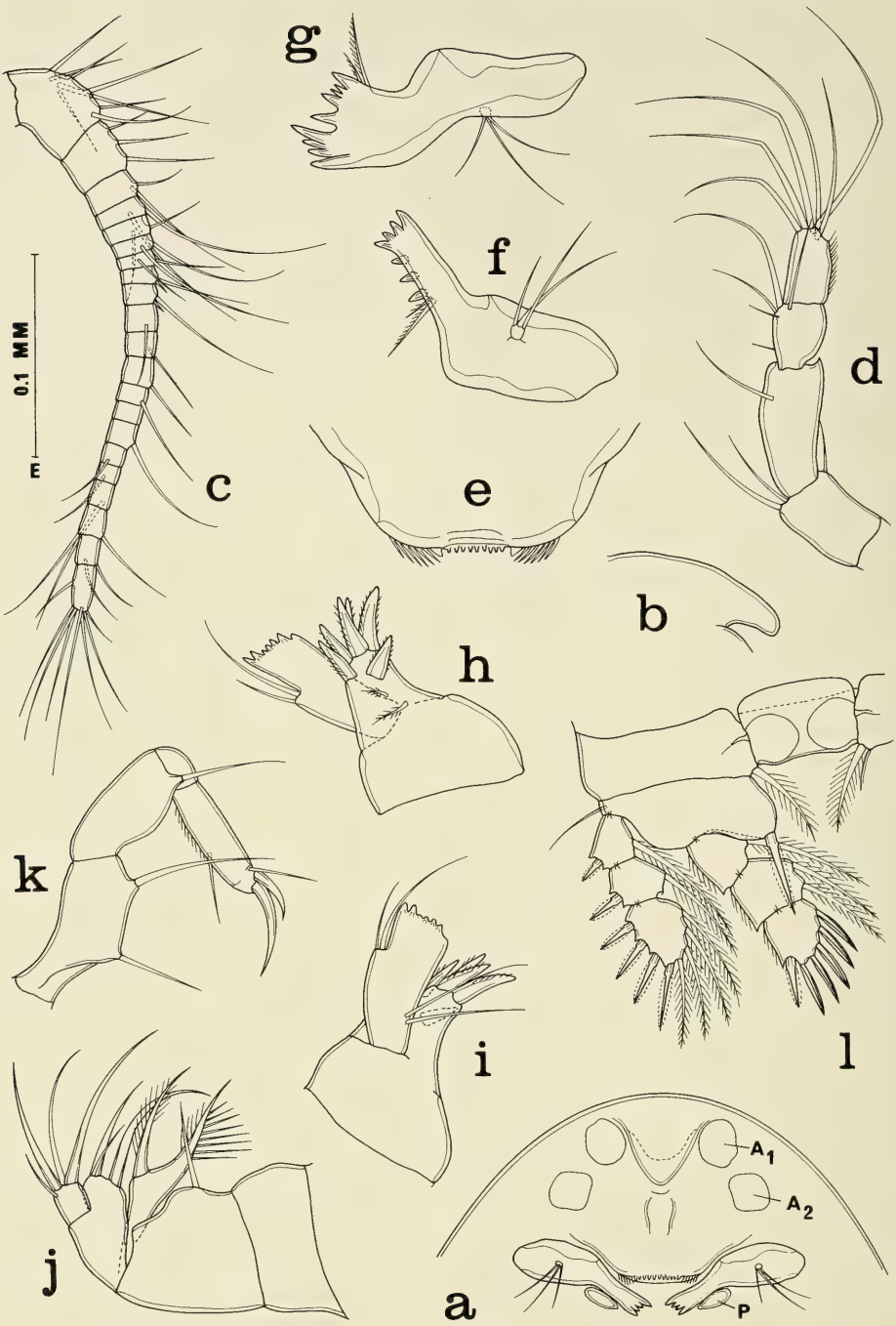


Fig. 2. *Euryte bellatula,* female. a, Rostrum, labrum, mandibles, and paragnaths, ventral (scale B); b, Outline of rostrum, lateral (B); c, First antenna, anterodorsal (E); d, Second antenna, postero-inner (E); e, Labrum, ventral (C); f, Mandible, ventral (C); g, Mandible, flat inner view (C); h, First maxilla, inner (C); i, First maxilla, outer (C); j, Second maxilla, inner (C); k, Maxilliped, inner (C); l, Leg 1 and intercoxal plate, anterior (E).

flanked by few setules. Mandible (Fig. 2a, f, g) 105 μm long with several unequal terminal teeth (in groups of 4 and 5) and 2 unilaterally barbed setae, and having small 1-segmented palp bearing 3 smooth setae. Paragnath small lobe posterior to mandible (Fig. 2a). First maxilla (Fig. 2h, i) with proximal part (gnathobase) having 6 barbed spines and 2 setae with lateral setules, distal part (palp) forming broad lobe with several terminal denticles and 2 pairs of smooth setae. Second maxilla (Fig. 2j) with first segment (praecoxa) unarmed, second segment (coxa) with 1 seta and distal inward expansion having 2 setae bearing lateral setules and forming forceps, third segment (basis) with 3 setae, and small fourth segment (exopod) with 3 long setae and 1 short seta. Maxilliped (Fig. 2k) 3-segmented, first segment (coxa) with 2 setae, second segment (basis) with 1 seta, third segment (endopod) elongate (possibly 3-segmented but divisions obscure) and having terminally 2 clawlike setae and 1 straight seta, and 1 seta and row of spinules on inner margin.

Legs 1–4 (Figs. 2l, 3a–c) biramous with 3-segmented rami. Spine and setal formula as follows:

P_1 coxa 0-1 basis 1-I	exp I-1;	I-1;	III,I,4
	enp 0-1;	0-2;	I,II,III
P_2 coxa 0-1 basis 1-0	exp I-1;	I-1;	III,I,IV,1
	enp 0-1;	0-2;	I,II,III
P_3 coxa 0-1 basis 1-0	exp I-1;	I-1;	III,I,V
	enp 0-1;	0-2;	I,II,III
P_4 coxa 0-1 basis 1-0	exp I-1;	I-1;	II,I,V
	enp 0-1;	0-2;	I,II,II

Leg 1 with basis having inner fringed spine 39 μm long. Rami with outer spines fringed, inner spines narrowly lamellate. Third segment of exopod of leg 2 notable in having formula III,I,IV,1.

Leg 5 (Fig. 1e) ventrally placed and united midventrally by narrow sclerite. First segment 26 × 15 μm with 1 short dorsal seta. Second segment elongate, 49 × 13 μm, unornamented, with 1 outer lateral fringed spine 52 μm, and terminally with 2 fringed spines 65 μm (outer) and 78 μm (inner) and 1 smooth seta 57 μm between them.

Leg 6 probably represented by 2 setae on genital area (Fig. 1d).

Color of living specimens unknown.

Male.—Body (Fig. 3d) slender. Length 0.59 mm (0.55–0.61 mm) and greatest width 0.20 mm (0.18–0.22 mm), based on 4 specimens. Greatest dorsoventral thickness 0.16 mm. Ratio of length to width of prosome 1.89:1. Ratio of length of prosome to that of urosome 1.32:1.

Segment bearing leg 5 (Fig. 3e) 31 × 67 μm. Genital segment 44 × 57 μm, only little wider than long. Four postgenital segments from anterior to posterior 34 × 42, 30 × 39, 24 × 35, and 29 × 34 μm.

Caudal ramus resembling that of female but smaller, 44 × 15 μm, ratio 2.93:1.

Body surface unornamented as in female.

Rostrum similar to that of female. First antenna (Fig. 3f) 210 μm long, 15-segmented, slightly modified. Lengths of segments: 26 (43 μm along anterior margin), 16, 15, 5, 4, 4, 9, 8, 3, 23, 10, 10, 21, 23, and 29 μm, respectively. Armature: 8, 3, 2, 2 + 1 aesthete, 2, 2, 2, 2, 2, 1, 2 + 1 aesthete, 2, 1, 3, and 8 + 1 aesthete. All setae smooth. Second antenna as in female.

Labrum, mandible, paragnath, first maxilla, second maxilla, maxilliped, and legs 1–4 like those of female.

Leg 5 (Fig. 3g) resembling that of female, similarly placed, second segment 33 × 12 μm.

Leg 6 (Fig. 3h, i) posteroventral flap on genital segment bearing fringed spine 15 μm and 2 slender setae approximately 11 μm.

Spermatophore not seen.

Color unknown.

Etymology.—The specific name *bellatula,* Latin meaning pretty or charming, alludes to the svelte appearance of this species.

Remarks.—Vervoort (1964:39) listed six nominal species, one variety and one undetermined species in the genus *Euryte,* and described one new species, *Euryte pseudo-*

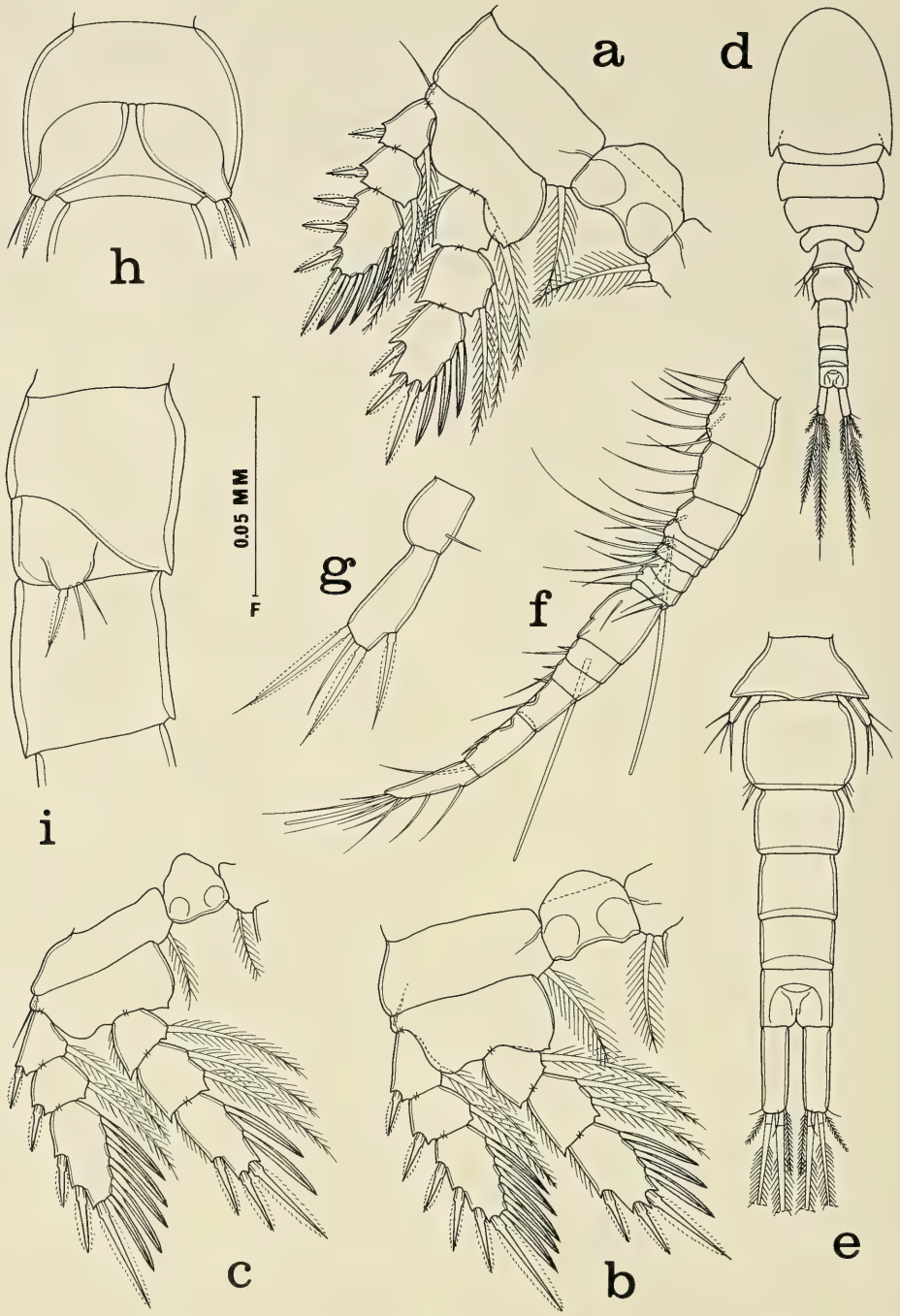


Fig. 3. *Euryte bellatula.* Female. a, Leg 2 and intercoxal plate, anterior (scale E); b, Leg 3 and intercoxal plate, anterior (E); c, Leg 4 and intercoxal plate, anterior (E). Male: d, Dorsal (A); e, Urosome, dorsal (E); f, First antenna, dorsal (C); g, Leg 5, lateral (F); h, Genital segment with leg 6, ventral (F); i, Genital segment and first postgenital segment, lateral (F).

robusta. Ummerkutty (1970) listed eight species and one variety. As far as can be determined, no new species have been added in recent years, and the number of congeners remains at eight or nine, depending upon whether varieties are treated as species.

Euryte bellatula differs from all previously described species in the genus. The formula III,I,IV,1 for the third segment of the exopod of leg 2 distinguishes the new species from *Euryte robusta* Giesbrecht, 1900 (length of the female 1.20–1.40 mm, Sars 1913), *E. curticornis* Sars, 1913 (short first antenna, Sars 1913, pl. XIV), and *E. pseudorobusta* Vervoort, 1964 (short caudal ramus, 2:1, Vervoort 1964), all of which have the formula III,I,V for the third segment of the exopod of leg 2. *Euryte brevicauda* Sewell, 1949, has a caudal ramus about 1.5:1 (Sewell 1949:35). *Euryte similis* T. Scott, 1912, has a more robust distal segment in leg 5 of the female, and has the formula I,II,III for the third segment of the endopod of leg 4 (T. Scott 1912, pl. 1, 21, 22). *Euryte longicauda* Philippi, 1843, has long caudal rami, about 9:1 (Sars 1913, pl. XII).

Order Poecilostomatoida Thorell, 1859
Family Lichomolgidae Kossmann, 1877
Genus *Haplomolgus* Humes & Ho, 1968
Haplomolgus incolumis, new species
Figs. 4, 5, 6

Type material.—128 ♀, 51 ♂ from *Montipora caliculata* (Dana), in 1.5 m, Ricaudy Reef, near Noumea, New Caledonia, 22°19′00″S, 166°27′18″E, 25 Jun 1971. Holotype ♀ (USNM 254471), allotype (USNM 254470), and 167 paratypes (122 ♀, 45 ♂) (USNM 254469) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Remaining paratypes in the collection of the author.

Female.—Body (Fig. 4a) elongate, prosome moderately broad. Length 1.19 mm (1.11–1.24 mm) and greatest width 0.43 mm (0.41–0.44 mm), based on 10 specimens. Greatest dorsoventral thickness 0.35 mm. Epimera of segments bearing legs 1–4 rounded. Segment bearing leg 1 fused with cephalosome. Ratio of length to width of prosome 1.68:1. Ratio of length of prosome to that of urosome 1.26:1.

Segment bearing leg 5 (Fig. 4b) 104 × 221 μm. Genital segment in dorsal view subquadrate, 138 × 151 μm, little wider than long, in lateral view notched dorsally (Fig. 4c). Genital areas situated dorsolaterally in anterior half of segment and connected by transverse, very broadly U-shaped bar. Each area with 2 minute setae approximately 5 μm (Fig. 4c). Three postgenital segments from anterior to posterior 78 × 104, 81 × 99, and 52 × 65 μm.

Caudal ramus (Fig. 4d) elongate, 117 × 21 μm, width taken at middle, ratio 5.57:1. Outer lateral seta 57 μm, dorsal seta 73 μm, outermost terminal seta 52 μm, innermost terminal seta 92 μm, and 2 median terminal seta 185 μm (outer) and 220 μm (inner). All setae smooth.

Egg sac containing 1 egg 153 × 125 μm (Fig. 4e), 135 × 122 μm (Fig. 4f), 187 × 135 μm (Fig. 4g), 2 eggs 159 × 140 μm (Fig. 4h), 3 eggs (Fig. 4i), or 4 eggs (Fig. 4j).

Rostrum (Fig. 4k) moderately elongate, linguiform. First antenna (Fig. 4l) 280 μm long. Lengths of its 7 segments: 24 (55 μm along anterior margin), 88, 23, 26, 40, 27, and 21 μm, respectively. Armature: 4, 13, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All setae smooth.

Second antenna (Fig. 4m) 4-segmented, 185 μm long and moderately robust, second segment 49 μm wide. Armature: 1, 1, 3, and 1 terminal claw 30 μm (Fig. 4n).

Labrum (Fig. 5a) triangular with widely separated ventrolateral lobes. Mandible (Fig. 5b) with slender recurved basal part leading to inner lobe with row of slender setules and to outer scalelike area with few small spinules joined to prominent hyaline posteriorly directed process. Lash long and barbed.

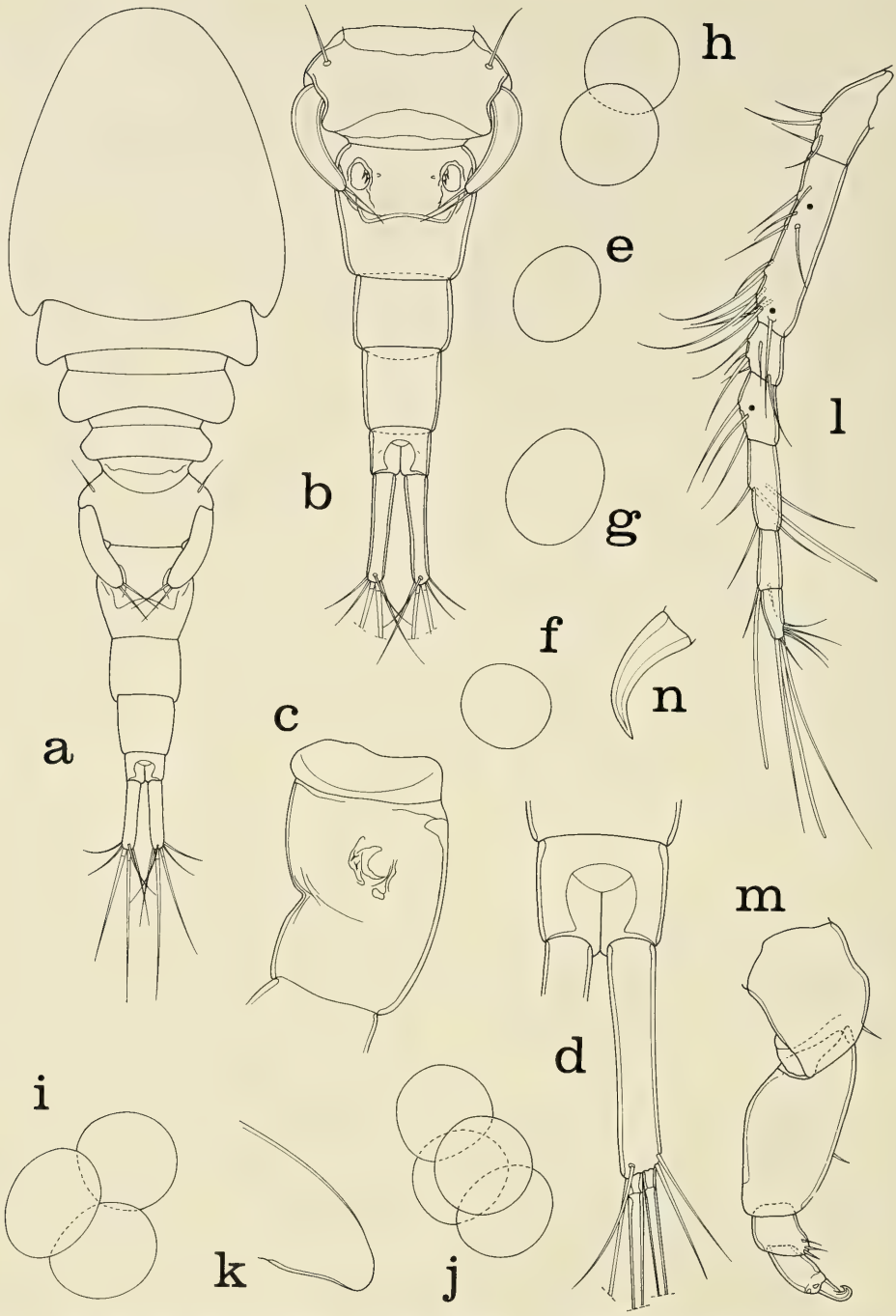


Fig. 4. *Haplomolgus incolumis,* female. a, Dorsal (scale A); b, Urosome, dorsal (D); c, Genital segment, lateral (B); d, Anal segment and caudal ramus, dorsal (E); e, Egg sac, ventral (A); f, Egg sac, ventral (A); g, Egg sac, ventrolateral (A); h, Egg sac, ventral (A); i, Egg sac, ventral (A); j, Egg sac, ventral (A); k, Outline of rostrum, lateral (E); l, First antenna, with 3 dots showing positions of aesthetes added in male, dorsal (E); m, Second antenna, dorsal (E); n, Claw of second antenna, flat view (F).

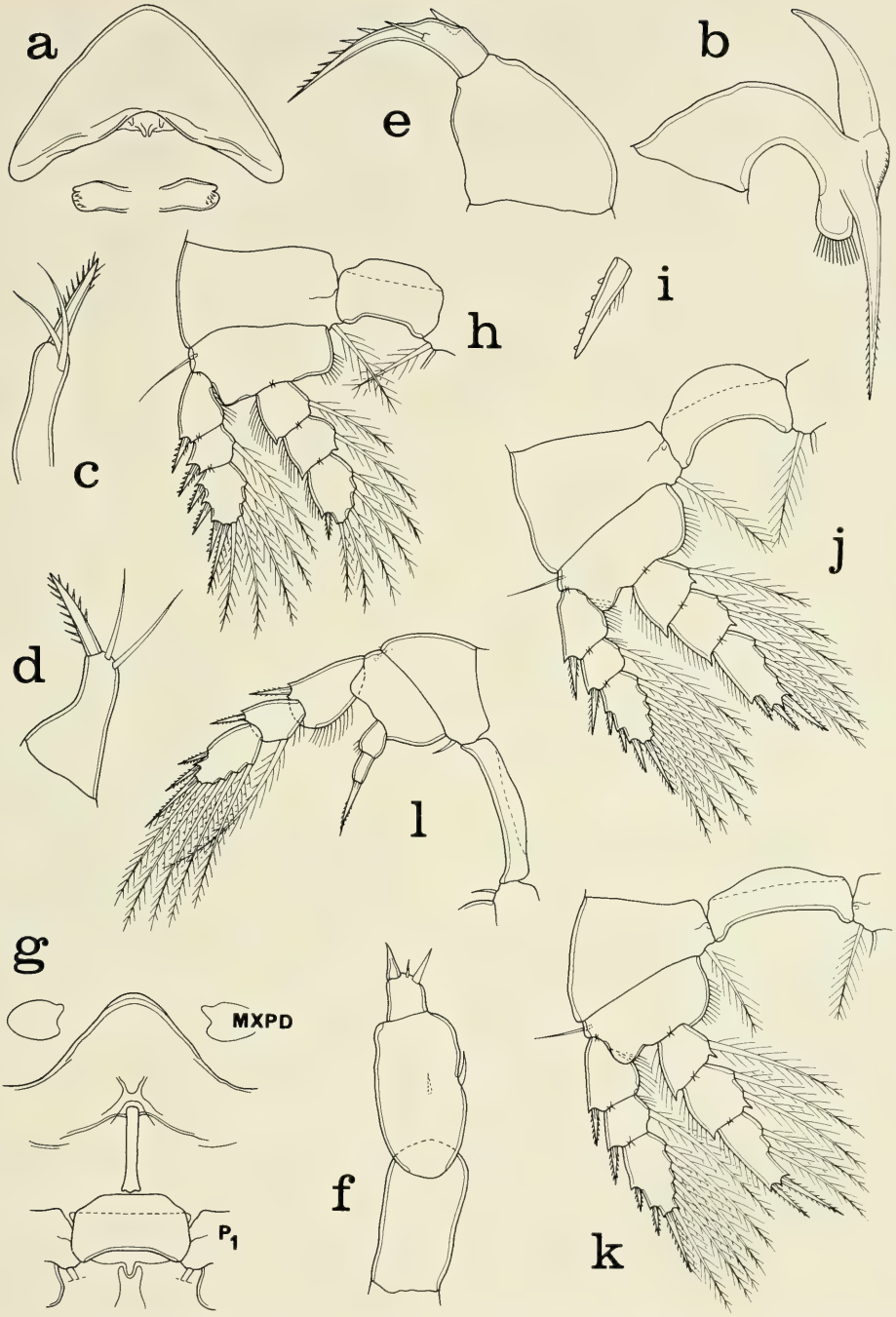


Fig. 5. *Haplomolgus incolumis,* female. a, Labrum and paragnaths, ventral (scale E); b, Mandible, posterior (F); c, First maxilla, outer (F); d, First maxilla, posterior (F); e, Second maxilla, antero-inner (C); f, Maxilliped, postero-outer (C); g, Region between maxillipeds and leg 1, ventral (B); h, Leg 1 and intercoxal plate, anterior (B); i, Outer spine on first segment of exopod of leg 1, anterior (C); j, Leg 2 and intercoxal plate, anterior (B); k, Leg 3 and intercoxal plate, anterior (B); l, Leg 4 and intercoxal plate, anterior (B).

Paragnath (Fig. 5a) small lobe with several minute spinules. First maxilla (Fig. 5c, d) with 2 smooth setae and 1 barbed spine. Second maxilla (Fig. 5e) with first segment unarmed, second segment with 2 unequal smooth setae and lash with prominent unilateral spines. Maxilliped (Fig. 5f) 3-segmented, first segment unarmed, second segment with 2 small setae, and third segment with 2 unequal setae and 1 terminal spiniform seta.

Ventral area between maxillipeds and first pair of legs not protuberant, with elongate narrow sclerite anterior to intercoxal plate of leg 1 (Fig. 5g).

Legs 1–4 (Fig. 5h, j–l) with 3-segmented rami except for 2-segmented endopod of leg 4. Formula for armature as follows:

P_1 coxa 0-1 basis 1-0	exp I-0; I-1;	III,I,4
	enp 0-1; 0-1;	I,2,3
P_2 coxa 0-1 basis 1-0	exp I-0; I-1;	III,I,5
	enp 0-1; 0-2;	I,II,3
P_3 coxa 0-1 basis 1-0	exp I-0; I-1;	II,I,5
	enp 0-1; 0-2;	II,2
P_4 coxa 0-1 basis 1-0	exp I-0; I-1;	II,I,5
	enp 0-0;	I

Inner margin of coxa in legs 1–3 with prominent plumose seta but this seta in leg 4 reduced, 18 μm long, and smooth. Exopod of leg 1 with outer spines bearing prominent spinules along proximal edges (Fig. 5i). Exopod of leg 4 143 μm long. Endopod (Fig. 6a) with first segment 23.5 × 18 μm and bearing few outer setules; second segment 21 × 8 μm, with terminal finely barbed spine 39 μm.

Leg 5 (Fig. 6b) with free segment elongate oval, 112 × 47 μm, slightly concave inwardly, unornamented, and bearing 2 subterminal smooth setae 55 μm and 61 μm. Adjacent smooth dorsal seta 65 μm, directed anterodorsally.

Leg 6 represented by 2 minute setae on genital area (Fig. 4c).

Color of living specimens slightly opaque gray, eye red.

Male.—Body (Fig. 6c) resembling that of female in general form. Length 1.22 mm (1.16–1.27 mm) and greatest width 0.41 mm (0.39–0.44 mm), based on 10 specimens. Greatest dorsoventral thickness 0.31 mm. Ratio of length to width of prosome 1.45:1. Ratio of length of prosome to that of urosome 1.06:1.

Segment bearing leg 5 (Fig. 6d) 65 × 164 μm. Genital segment in dorsal view 226 × 244 μm, slightly wider than long. Four postgenital segments from anterior to posterior 57 × 75, 62 × 74, 81 × 65, and 52 × 62 μm.

Caudal ramus (Fig. 6d) resembling that of female but smaller, 107 × 22 μm, ratio 4.86:1.

Rostrum like that of female. First antenna segmented and armed as in female, but 3 very long aesthetes added (at points indicated by dots in Fig. 4l), so that formula is 4, 13 + 2 aesthetes, 6 , 3 + 1 aesthete, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. Longest aesthete, that on proximal part of second segment, 235 μm long (compared with 320 μm for entire length of first antenna). Second antenna (Fig. 6e) resembling that of female, but less robust, width of second segment 39 μm.

Labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 6f) elongate. First segment unarmed. Second segment with 2 inner setae and group of spines (Fig. 6g). Small third segment unarmed. Claw 234 μm long, with 2 unequal proximal setae and bearing minute denticles along slightly concave margin.

Ventral area between maxillipeds and first pair of legs as in female.

Legs 1–4 similar to those of female, but third segment of endopod of leg 1 with formula I,I,4 (Fig. 6h) with spiniform processes at both sides of inner spine. Leg 4 with endopod like that of female, but in 1 male right endopod with narrow second segment (Fig. 6i) and in another male right endopod with formula 0-0; 0 and left endopod with 0-1; I (Fig. 6j).

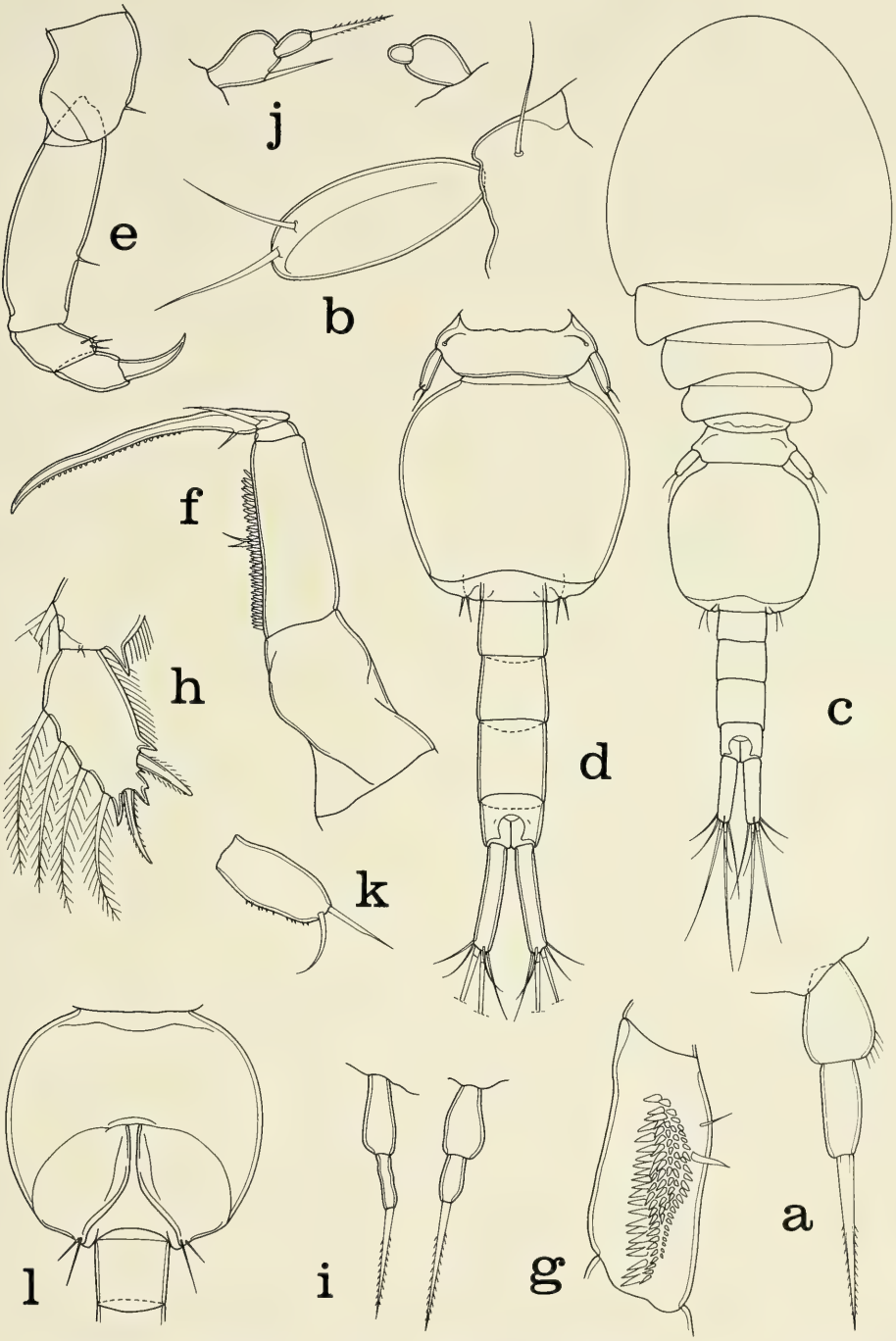


Fig. 6. *Haplomolgus incolumis.* Female: a, Endopod of leg 4, anterior (scale F); b, Leg 5, dorsal (E). Male: c, Dorsal (A); d, Urosome, dorsal (D); e, Second antenna, dorsal (E); f, Maxilliped, postero-inner (B); g, Second segment of maxilliped, inner (E); h, Third segment of endopod of leg 1, anterior (C); i, Pair of abnormal endopods of leg 4, ventral (C); j, Pair of abnormal endopods of leg 4, ventral (C); k, Free segment of leg 5, dorsal (C); l, Genital and first postgenital segments, ventral (D).

Leg 5 (Fig. 6k) with free segment smaller than in female, 39 × 21 μm, and having few minute spinules along outer border.

Leg 6 (Fig. 6l) posteroventral flap on genital segment bearing 2 small setae.

Spermatophore not seen.

Color of living specimens as in female.

Etymology.—The specific name *incolumis,* Latin meaning unimpaired or undiminished, alludes to the full expression of the endopod of leg 4 in this species.

Remarks.—Two species of *Haplomolgus* Humes & Ho, 1968b, have been described, both associated with the scleractinian genus *Montipora* in Madagascar and Ceram (see Humes & Ho 1968b, Humes 1978).

Haplomolgus incolumis differs from *Haplomolgus montiporae* Humes & Ho, 1968b, in the larger size of the female, the longer female caudal ramus, the endopod of leg 4 with 0-0; I, and the free segment of the female leg 5 being longer, 112 × 47 μm. Furthermore, in contrast to the new species, *H. montiporae* has 4 setae on the first maxilla and there is only slight sexual dimorphism (I,5) in the third segment of the endopod of leg 1. *Haplomolgus subdeficiens* Humes, 1978, has the formula I,2 for the third segment of the endopod of leg 3; the male of this species is unknown.

The 2-segmented endopod of leg 4 in *Haplomolgus incolumis,* armed as 0-0; I, is similar to the condition in the genus *Monomolgus* Humes & Frost, 1964. However, the two genera are distinct in the form of the mandible, the posteriorly directed process in *Haplomolgus* being absent in *Monomolgus.*

Haplomolgus montiporae Humes & Ho, 1968

Specimens studied.—From New Caledonia: 607 ♀, 105 ♂ from *Montipora lobulata* Bernard, in 0.5 m, Rocher à la Voile, Noumea, 22°18′24″S, 166°25′50″E, 17 Jun 1971; 4 ♀, 1 ♂ from *Montipora lobulata,* in 0.5 m, Rocher à la Voile, Noumea; 136 ♀, 129 ♂ from *Montipora ramosa* Bernard, in 2 m, between Isle Noumbo and Isle N'Die, Baie Dumbea, near Noumea, 22°12′47″S, 166°24′41″E, 9 Jul 1971; 219 ♀, 105 ♂ from *Montipora ramosa,* in 2 m, north of Isle Maître, near Noumea, 22°19′30″S, 166°24′35″E, 13 Jul 1971; 62 ♀, 24 ♂ from *Montipora composita* Crossland, in 2 m, Ricaudy Reef, near Noumea, 22°19′00″S, 166°26′44″E, 25 Jun 1971.

From northeastern Australia: 16 ♀, 5 ♂ from *Montipora composita,* in 2 m, Mermaid Cove, Lizard Island, 14°39′50″S, 145°27′00″E, 27 Oct 1982; 11 ♀, 9 ♂ from *Montipora verrilli* Vaughan, in 3 m, Mermaid Cove, Lizard Island, 27 Oct 1982.

Remarks.—*Haplomolgus montiporae* has been previously reported to be associated with *Montipora compressa* in the Moluccas (Humes 1978) and with *Montipora sinensis, Montipora* sp. cf. *M. stellata* and *Montipora* sp. in Madagascar (Humes & Ho 1968b, Humes & Stock 1973).

Genus *Odontomolgus* Humes & Stock, 1972

Odontomolgus forhani Humes, 1978

Specimens studied.—From New Caledonia: 13 ♀, 5 ♂ from *Montipora composita* Crossland, in 2 m, Ricaudy Reef, near Noumea, 22°19′00″S, 166°26′44″E, 25 Jun 1971; 3 ♀ from *Montipora ramosa* Bernard, in 2 m, north of Isle Maître, near Noumea, 22°19′30″S, 166°24′35″E, 13 Jul 1971; 1 ♀ from *Montipora lobulata* Bernard, in 0.5 m, Rocher à la Voile, Noumea, 22°18′24″S, 166°25′50″E, 17 Jun 1971.

From the Moluccas: 17 ♀, 8 ♂ from *Montipora* sp. cf. *M. undata* Bernard, in 10 m, Poelau Parang, eastern Ceram, 03°17′00″S, 130°44′48″E, 23 May 1975.

From northeastern Australia: 4 ♀, 1 ♂ from *Montipora composita,* in 2 m, Mermaid Cove, Lizard Island, 14°39′50″S, 145°27′00″E, 27 Oct 1982; 1 ♀ from *Montipora verrilli* Vaughan, in 3 m, Mermaid Cove, Lizard Island, 27 Oct 1982.

Remarks.—*Odontomolgus forhani* has

been previously reported from *Montipora compressa* and *Montipora prolifera* in the Moluccas (Humes 1978).

Order Siphonostomatoida Thorell, 1859
Family Asterocheridae Giesbrecht, 1899
Hetairosyna, new genus

Diagnosis.—Asterocheridae. Female: Two postgenital segments. Siphon short, reaching only to maxillipeds. First antenna 19-segmented, with aesthete on segment 17. Second antenna with very small 1-segmented exopod, terminal segment of endopod with claw and 1 seta. Mandible with 1-segmented palp bearing 1 long seta. Leg 1 with first segment of exopod having inner seta, third segment of exopod having very small proximal vestigial outer spine, with formula III,I,4, or this spine absent, II,I,4. Legs 1–3 with third segment of endopod having I,II,3, that of segment of leg 4 with I,II,2. Leg 4 with third segment of exopod having III,I,4. Free segment of leg 5 with 3 setae.

Male: Three postgenital segments. First antenna 16-segmented, with aesthete on segment 15. Strong sexual dimorphism in endopod of leg 3.

Type species.—*Hetairosyna terpna,* new species.

Gender.—Feminine.

Etymology.—The generic name *Hetairosyna,* from the Greek words *hetairos,* a companion, and the suffix *-syne,* meaning condition, alludes to the association of members of this genus with corals.

Remarks.—*Hetairosyna,* though placed in the Asterocheridae following the brief diagnosis given by Stock (1987), differs from the more than 30 genera in the family. Most of these genera may be distinguished from *Hetairosyna* by means of the key to the genera provided by Stock (1987). Five genera need special attention, however, to distinguish them from the new genus. The salient characters separating them from *Hetairosyna* are as follows:

Asterocheres Boeck, 1859. The second antenna has three distal elements, the longest more or less setiform; the 1- or 2-segmented palp on the mandible has at least two long setae; and the third segment of the endopod of leg 4 has the formula 1-1 + I-2 (Stock 1987).

Asteropontius Thompson & A. Scott, 1903. The mandible has a short 1-segmented palp or the palp is absent, its seta reduced; the third segment of the endopod of leg 4 has 1-1 + I-2 (Stock 1975).

Asteropontella Stock, 1989. The third segment of the exopod of leg 4 has I,I,3 or II,I,3; the third segment of the exopod of legs 1–3 has 2 lateral spines; the exopod of the second antenna is vestigial (Stock 1989).

Asteropontoides Stock, 1975. The first antenna of the female has an aesthete on the penultimate segment; in leg 4 the third segment of the endopod has 1,I,2 and the third segment of the exopod has III,I,3 (Sewell 1949, Stock 1975).

Asteropontopsis Stock, 1987. The third segment of the exopod of leg 3 has II,I,4; the third segment of the endopod of leg 3 has 1,1 + I,3 (Stock 1987).

Hetairosyna terpna new species
Figs. 7, 8, 9, 10

Type material.—43 ♀, 40 ♂ from *Montipora caliculata* (Dana), in 1.5 m, Ricaudy Reef, near Noumea, New Caledonia, 22°19′00″S, 166°26′44″E, 25 Jun 1971. Holotype ♀ (USNM 254462), allotype (USNM 254463), and 75 paratypes (38 ♀, 37 ♂) (USNM 254461) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Remaining paratypes (dissected) in the collection of the author.

Other specimens.—From New Caledonia: 11 ♀ from *Montipora composita* Crossland, in 2 m, Ricaudy Reef, near Noumea, 25 Jun 1971; 3 ♀ from *Montipora ramosa* Bernard, in 2 m, north of Isle Maître, near Noumea, 22°19′30″S, 166°24′35″E, 13 Jul 1971; 30

♀, 13 ♂ from *Montipora lobulata* Bernard, in 0.5 m, Rocher à la Voile, Noumea, 22°18′24″S, 166°25′50″E, 17 Jun 1971; 93 ♀ from *Montipora* sp. cf. *M. efflorescens* Bernard, in 1 m, east of Isle N'Die, Baie Dumbea, near Noumea, 22°13′15″S, 166°24′26″E, 6 Jul 1971.

From the Moluccas: 14 ♀ from *Montipora compressa* (Esper), in 2 m, Natsepa, Ambon, 03°37′05″S, 128°17′00″E, 28 May 1975; 3 ♀ from *Montipora prolifera* Brueggemann, in 3 m, southern shore of Goenoeng Api, Banda Islands, 04°32′05″S, 129°52′30″E, 26 Apr 1975.

From Enewetak Atoll, Marshall Islands: 17 ♀ from *Montipora ambigua* Bernard, in 3 m, south of Parry Island, 9 Jul 1969; 12 ♀ from *Montipora patula* Bernard, in 2 m, western end of Bogen Island, 23 Jun 1969.

From northeastern Australia: 8 ♀, 6 ♂ from *Montipora composita,* in 2 m, Mermaid Cove, Lizard Island, 14°39′50″S, 145°27′00″E, 27 Oct 1982.

From Madagascar: 41 ♀, 4 ♂ from *Montipora* sp., west of Pte de Tafondro, Nosy Bé, 3 Dec 1963; 3 ♀ from *Montipora sinensis* Bernard, in 1 m, Nosy Taolankena, near Nosy Bé, 15 Nov 1963; 12 ♀, 2 ♂ from *Montipora* sp. cf. *M. stellata* Bernard, in 2 m, off Ampombilava, Nosy Bé, 26 Sept 1964.

Female.—Body (Fig. 7a) with broad prosome covered with minute hyaline scales. Length 0.92 mm (0.88–1.01 mm) and greatest width 0.49 mm (0.47–0.52 mm), based on 10 specimens. Greatest dorsoventral thickness 0.33 mm. Epimera of segments bearing legs 1–4 rounded in dorsal view, weakly pointed in lateral view. Dorsal part of segment bearing leg 3 partly covering segment bearing leg 4. Segment bearing leg 1 not separated dorsally from cephalosome. Ratio of length to width of prosome 1.29:1. Ratio of length of prosome to that of urosome 2.09:1.

Segment bearing leg 5 (Fig. 7b) 60 × 152 μm. Genital segment slightly expanded in anterior third, 153 × 127 μm in greatest dimensions in dorsal view, 91 μm wide in posterior third. Genital areas located dorsolaterally in anterior third. Each area (Fig. 7b–d) with 2 very small setae. Surfaces of all urosomal segments covered with minute hyaline scales (Fig. 7b–d). Genital segment with row of long setules laterally posterior to expansion (Fig. 7d). Two postgenital segments, first segment 62 × 78 μm, second segment 50 × 75 μm.

Caudal ramus (Fig. 7e) short, trapezoidal, wider than long, 29 μm along outer edge, 18 μm along inner edge, and 36 μm in greatest width. Outer lateral seta placed dorsally, 107 μm, dorsal seta 72 μm, both smooth. Outermost terminal seta 156 μm, innermost terminal seta 195 μm, and 2 median terminal setae 273 μm (outer) and 330 μm (inner), swollen proximally. Ramus bearing few outer scales as on urosomal segments.

Dorsal surface of body without visible sensilla, but with minute scales.

Egg sac (Fig. 7f) 252 × 190 μm, containing 5 eggs, each about 135–140 μm in maximum diameter.

Rostral area weakly developed (Fig. 8a). First antenna (Fig. 8b) 418 μm long, 19-segmented. Length of segments: 23 (47 μm along anterior margin), 13, 10, 10, 10, 10, 11, 13, 10, 15.5, 26, 25, 29, 27, 29, 34, 37, 14, and 26 μm, respectively. Formula for armature: 1, 2, 2, 2, 2, 2, 2, 2, 6, 1 + 1 small spine, 2, 2, 2, 2, 2, 2, 2 + 1 aesthete, 3, and 7. All setae smooth.

Second antenna (Fig. 8c) 5-segmented, 257 μm long including claw. Coxa and basis unarmed. Exopod minute, 7 × 4 μm. Endopod with first segment elongate and unarmed, second segment with 1 seta, third segment with terminal claw 57 μm, 1 adjacent seta, and outer row of setules.

Siphon (Fig. 8d) short, approximately 165 μm long. Mandible (Fig. 8e) with long slender blade 143 μm, its tip dentate inwardly and expanded outwardly (Fig. 8f); palp 1-segmented with long slender seta, palp and seta together 91 μm. Both mandibles lying along sides of siphon (Fig. 8d). First maxilla (Fig. 8g) with 2 lobes, shorter outer lobe

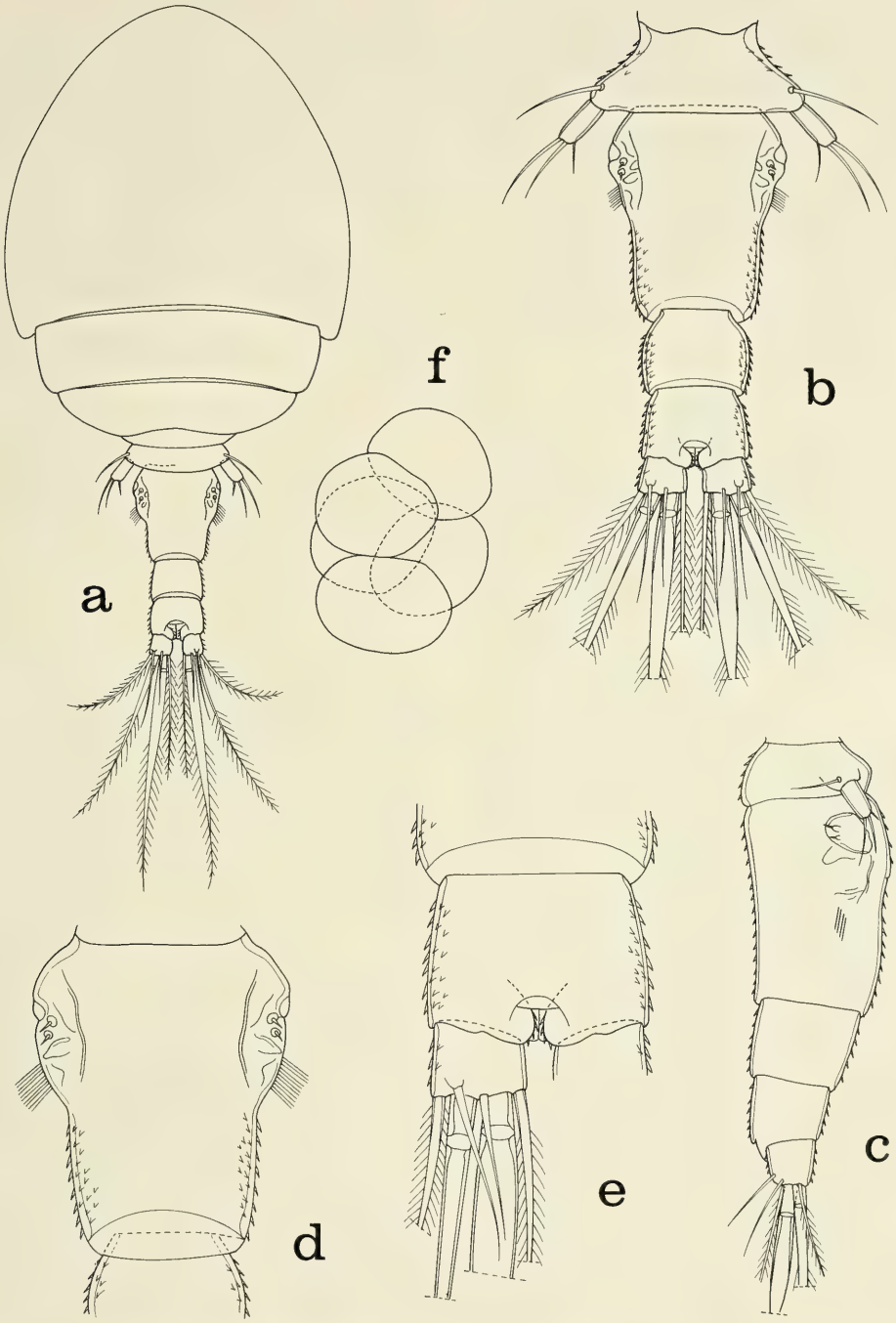


Fig. 7. *Hetairosyna terpna,* female. a, Dorsal (scale A); b, Urosome, dorsal (B); c, Urosome, lateral (B); d, Genital segment, dorsal (E); e, Anal segment and caudal ramus, dorsal (C); f, Egg sac, ventral (D). (In a–e scales not shown over entire surface.)

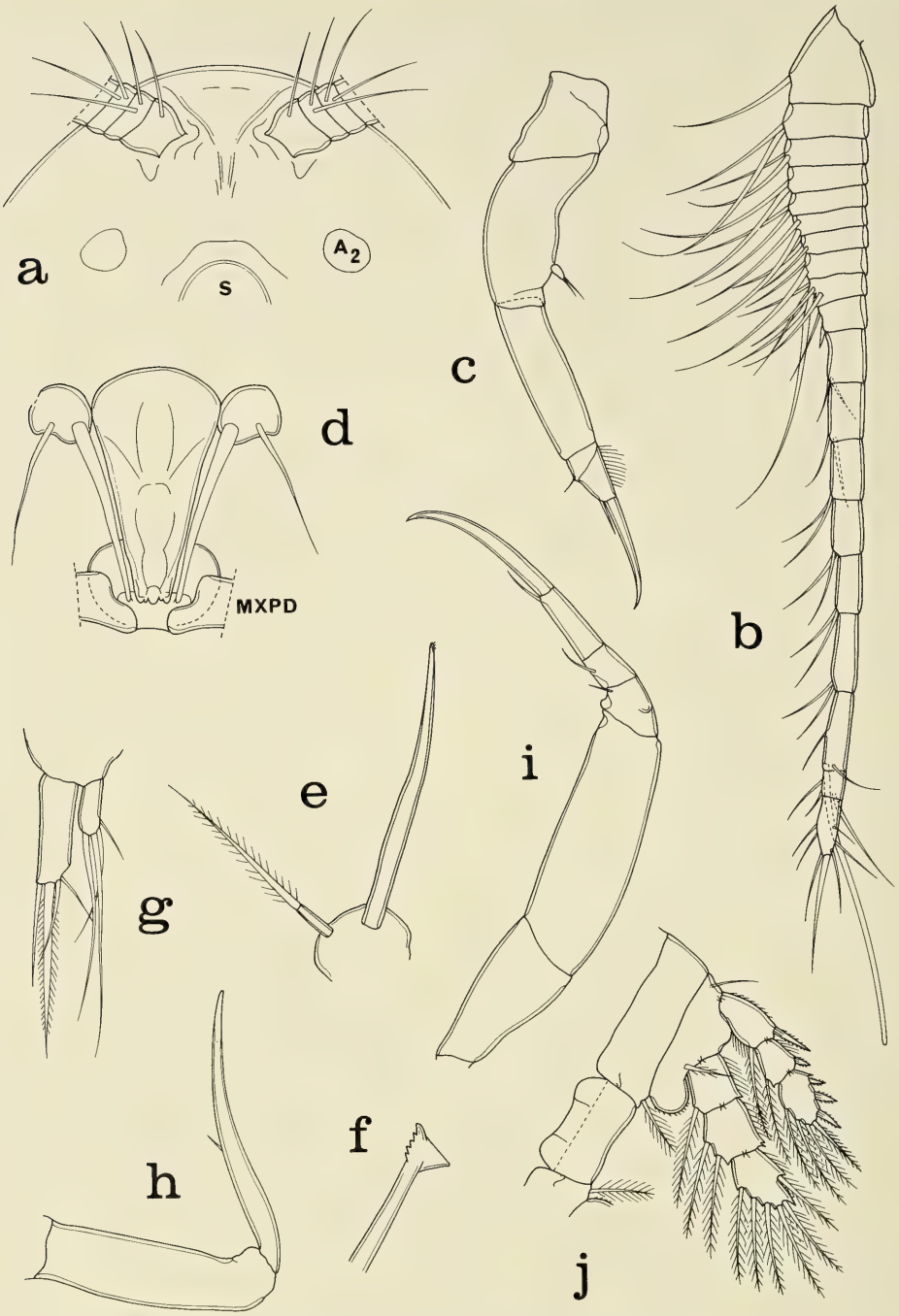


Fig. 8. *Hetairosyna terpna,* female. a, Rostral area, ventral (scale B); b, First antenna, anterodorsal (E); c, Second antenna (E); d, Siphon and mandibles, ventral (B); e, Mandible, anterior (E); f, Tip of mandible, posteroinner (F); g, First maxilla, posterior (E); h, Second maxilla, inner (E); i, Maxilliped, posterior (E); j, Leg 1 and intercoxal plate, anterior (B).

with 4 setae, longer inner lobe with 4 setae, 1 distinctly barbed. Second maxilla (Fig. 8h) 2-segmented, first segment unarmed, second segment clawlike with small seta at midlength. Maxilliped (Fig. 8i) 5-segmented, first and second segments unarmed, third, four, and fifth segments with 1 seta each, claw 70 μm.

Ventral region between maxillipeds and first pair of legs not protuberant.

Legs 1–4 (Figs. 8j, 9a–c) biramous, with 3-segmented rami. Formula for armature as follows:

P_1 coxa 0-1	basis 1-I	exp I-1;	I-1; III,I,4
		enp 0-1;	0-2; 1,2,3
P_2 coxa 0-1	basis 1-0	exp I-1;	I-1; III,I,4
		enp 0-1;	0-2; 1,II,3
P_3 coxa 0-1	basis 1-0	exp I-1;	I-1; III,I,4
		enp 0-1;	0-2; 1,II,3
P_4 coxa 0-1	basis 1-0	exp I-1;	I-1; III,I,4
		enp 0-1;	0-2; 1,II,2

Legs 1–3 with long plumose seta on inner side of coxa, but this seta reduced in leg 4. Inner element on basis setiform spine. Inner margin of basis in leg 1 with minute marginal spinules, but smooth in legs 2–4. Proximal outer spine on third segment of exopod of leg 1 very small, vestigial. In 1 female, right endopod of leg 1 with aberrant formula 0-2; 0-2; 1,2,3.

Leg 5 (Fig. 9d) with free segment 36 × 15.5 μm, with few minute scales on outer margin, its 3 setae 20, 55, and 65 μm, respectively. Adjacent dorsal seta 52 μm. All setae smooth.

Leg 6 represented by 2 minute setae on genital area (Fig. 7d).

Color of living specimens in transmitted light transparent to opaque gray, eye red.

Male.—Body (Fig. 9e) with prosome more slender than in female. Length 0.73 mm (0.70–0.78 mm) and greatest width 0.33 mm (0.31–0.35 mm), based on 10 specimens. Greatest dorsoventral thickness 0.25 mm. Epimeral areas slightly more pointed than in female. Ratio of length to width of prosome 1.49:1. Ratio of length of prosome to that of urosome 1.86:1. Urosomal segments with surficial scales as in female.

Caudal ramus (Fig. 9f) resembling that of female but smaller, 18 μm along outer edge, 11 μm along inner edge, and 26 μm wide.

Body surface as in female.

Rostral area like that of female. First antenna (Fig. 9g) 340 μm long, 16-segmented (though segment 10 possibly divided). Lengths of segments: 23 (38 μm along anterior margin), 13, 12, 12, 12, 12, 12, 12, 12, 16, 48, 15.5, 13, 40, 39, and 34 μm, respectively. Armature: 1, 2, 2, 2, 2, 2, 2, 2, 6, 1 + 1 small spine, 2, 1, 1, 0, 0 + 1 aesthete, and 7. Setae hyaline and difficult to observe.

Second antenna, siphon, mandible, first maxilla, and second maxilla as in female. Maxilliped (Fig. 9h) resembling that of female but showing sexual dimorphism in having inner spiniform process on both first and second segments.

Ventral area between maxillipeds and first pair of legs as in female.

Legs 1–4 segmented and armed as in female, but sexual dimorphism in legs 2 and 3. Endopod of leg 2 (Fig. 10a) with terminal spiniform process on third segment larger than in female. Endopod of leg 3 (Fig. 10b) with second segment having enlarged terminal outer process; third segment distinctly smaller than first two, with formula 1,II,3, but having enlarged swollen inner terminal process bearing 1 outer setule.

Leg 5 (Fig. 10c) with minute free segment 13 × 10 μm, bearing 3 setae as in female.

Leg 6 (Fig. 10d) posteroventral flap on genital segment bearing 2 setae 10 μm and 26 μm.

Spermatophore unknown.

Color as in female.

Etymology.—The specific name *terpna* is derived from the Greek word *terpnos*, meaning delightful, pleasing.

Remarks.—*Hetairosyna terpna* is associated with at least 11 species of *Montipora* from Madagascar to Enewetak Atoll to New Caledonia (Table 3).

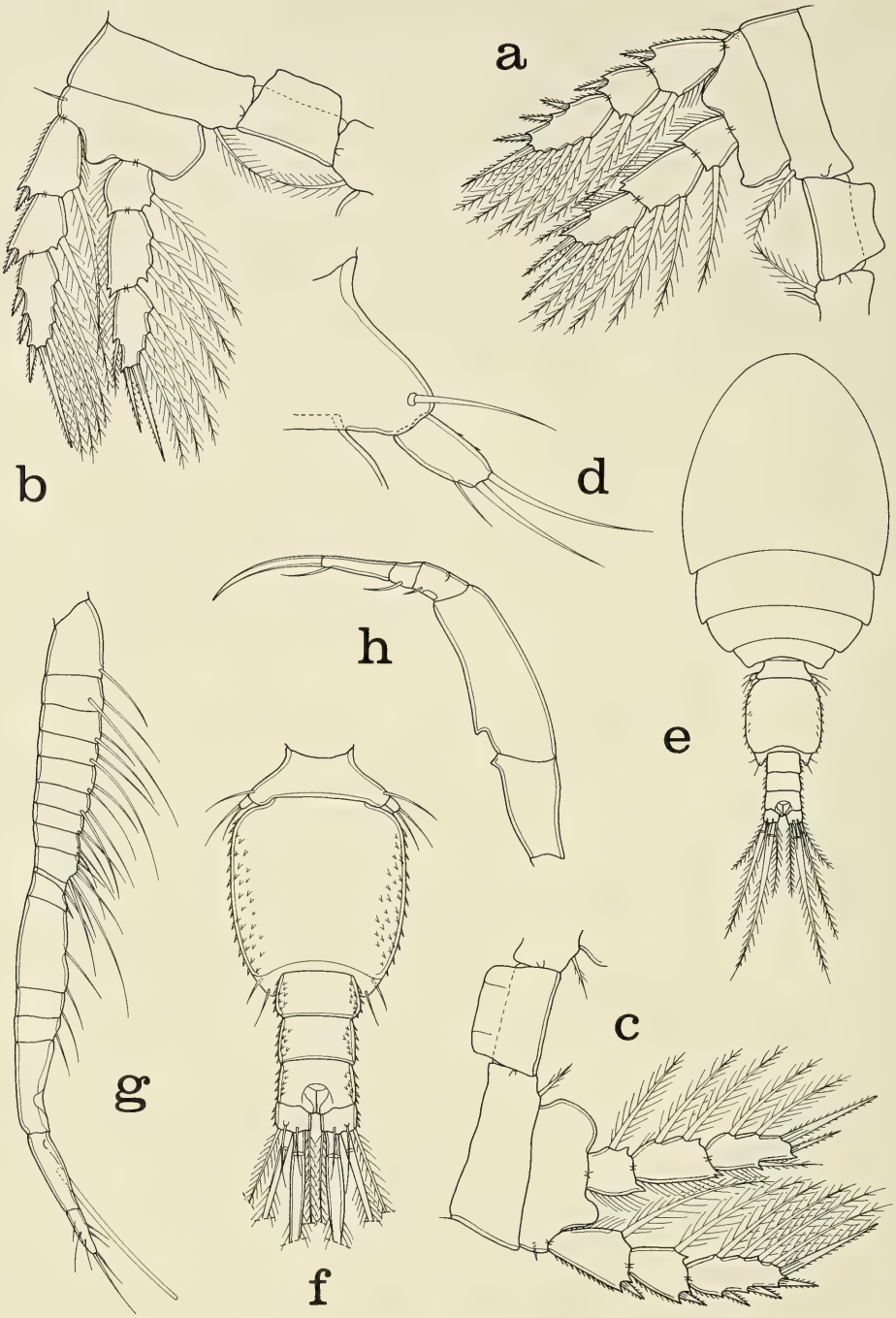


Fig. 9. *Hetairosyna terpna.* Female: a, Leg 2 and intercoxal plate, anterior (scale B); b, Leg 3 and intercoxal plate, anterior (B); c, Leg 4 and intercoxal plate, anterior (B); d, Leg 5, dorsal (C). Male: e, Dorsal (A); f, Urosome, lateral (B); g, First antenna, anterodorsal (E); h, Maxilliped, posterior (E).

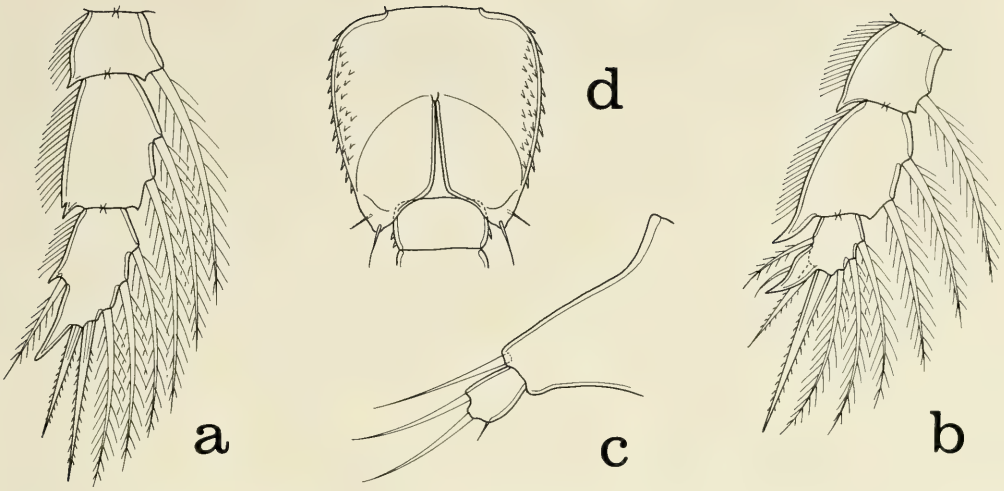


Fig. 10. *Hetairosyna terpna,* male. a, Endopod of leg 2, anterior (scale C); b, Endopod of leg 3, anterior (C); c, Leg 5, ventral (F); d, Genital segment, ventral (B).

Hetairosyna laciniata, new species
Figs. 11, 12, 13

Type material.—11 ♀, 6 ♂ from *Montipora caliculata* (Dana), in 1.5 m, Ricaudy Reef, near Noumea, New Caledonia, 22°19′00″S, 166°26′44″E, 25 Jun 1971. Holotype ♀ (USNM 254467), allotype (USNM 254468), and 11 paratypes (7 ♀, 4 ♂) (USNM 254466) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Remaining paratypes (dissected) in the collection of the author.

Other specimens.—From New Caledonia: 16 ♀, 5 ♂ from *Montipora composita,* in 2 m, Ricaudy Reef, near Noumea, 25 Jun 1971; 19 ♀, 17 ♂ from *Montipora ramosa* Bernard, in 2 m, north of Isle Maître, near Noumea, 22°19′30″S, 166°24′35″E, 13 Jul 1971; 27 ♀, 41 ♂ from *Montipora lobulata* Bernard, in 0.5 m, Rocher à la Voile, Noumea, 22°18′24″S, 166°25′50″E, 17 Jun 1971.

From Madagascar.—2 ♀, 2 ♂ from *Montipora sinensis* Bernard, in 1 m, Nosy Taolankena, near Nosy Bé, 15 Nov 1963.

Female.—Body (Fig. 11a) with unusually broad orbicular prosome. Length 0.87 mm (0.81–0.90 mm) and greatest width 0.58 mm (0.56–0.61 mm), based on 10 specimens. Greatest dorsoventral thickness 0.24 mm. Segment bearing leg 1 fused with cephalosome and finely serrate on lateral margins. Epimera of segments bearing legs 2–4 truncate and finely and irregularly serrate. Dorsal surface of prosome tessellated (Fig. 11b). Ratio of length to width of prosome 1.03:1. Ratio of length of prosome to that of urosome 1.86:1.

Segment bearing leg 5 (Fig. 11c) 73 × 150 μm. Genital segment 134 × 138 μm, nearly as long as wide in dorsal view, widest in anterior half. Row of several slender setules on both sides near middle of segment. Dorsal surface of segment with mostly crescentic sculpturing (Fig. 11d). Genital areas located dorsolaterally at expanded portion of segment. Each area with 2 minute setae and very small spinous process (Fig. 11d). Two postgenital segments, first segment 61 × 65 μm, second segment 55 × 57 μm, both with delicate minute scales laterally and continuing over dorsal surfaces.

Caudal ramus (Fig. 11e) short, 22 μm long on outer side, 19 μm long on inner side, and 24 μm wide. Outer lateral seta (placed dorsally) 20 μm, dorsal seta 20 μm, outermost terminal seta 44 μm, innermost terminal

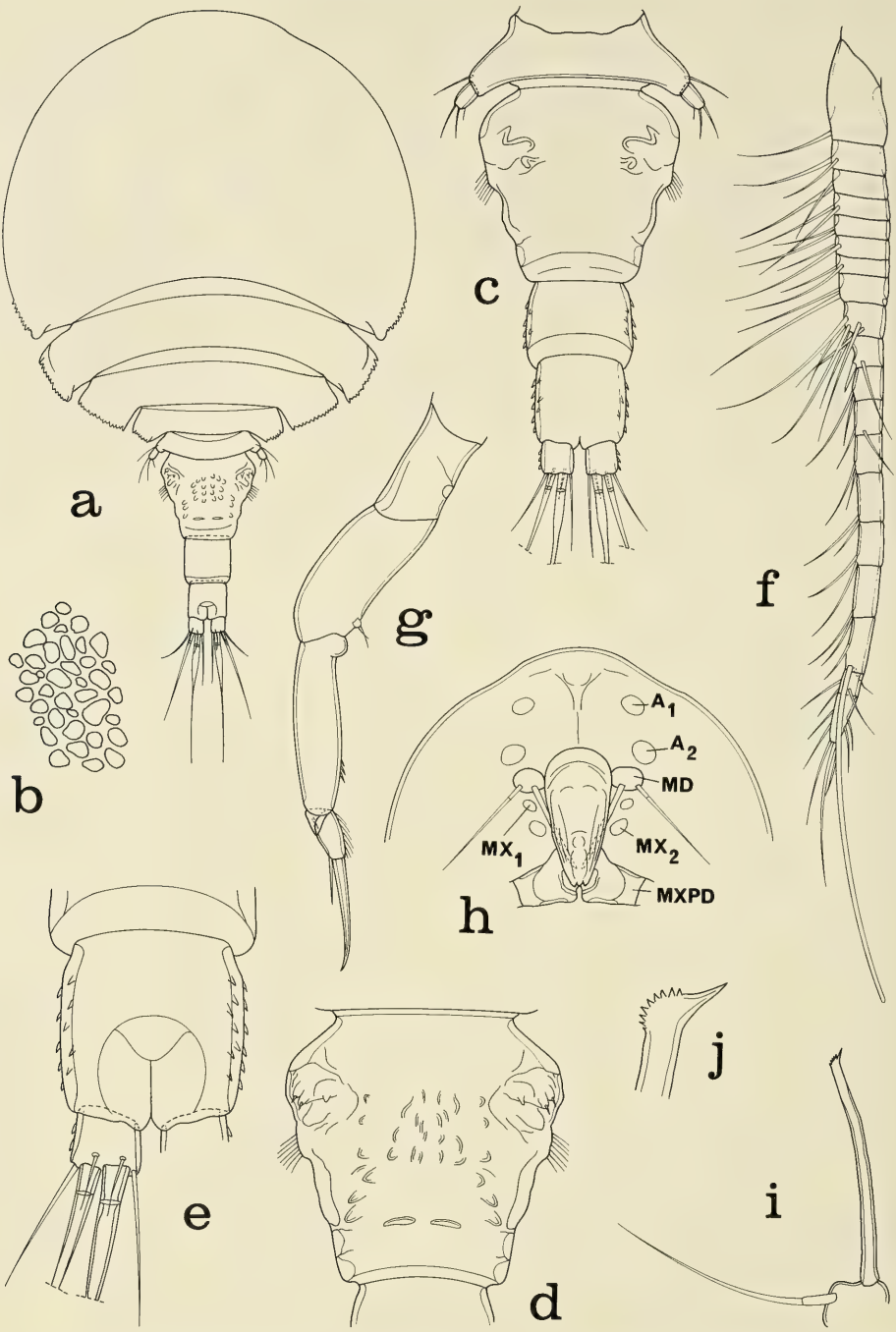


Fig. 11. *Hetairosyna laciniata,* female. a, Dorsal (scale A); b, Tessellations on surface of prosome, dorsal (E); c, Urosome, ventral (B); d, Genital segment, dorsal (B); e, Anal segment and caudal ramus, dorsal (C); f, First antenna, posteroventral (E); g, Second antenna, antero-outer (E); h, Rostral area and siphon, ventral (A); i, Mandible, anterior (B); j, Tip of mandible, flat view (C).

setae 73 μm, and 2 long median terminal setae, outer 570 μm, and inner (swollen proximally) 930 μm. All setae smooth. Few scales on outer surface of ramus.

Dorsal surface of body without visible sensilla, but prosome tessellated (Fig. 11b).

Egg sac not seen.

Rostral area weak (Fig. 11h). First antenna (Fig. 11f) 340 μm long, 19-segmented. Lengths of segments 26 (52 μm along anterior margin), 15, 11, 10, 10, 11, 10, 13, 13, 13, 14, 14, 18, 21, 22, 22, 28, 14, and 19 μm, respectively. Armature: 1, 2, 2, 2, 2, 2, 2, 2, 6, 1 + 1 small spine, 2, 2, 2, 2, 2, 2, 2 + 1 aesthete, 3, and 7. All setae smooth.

Second antenna (Fig. 11g) probably 5-segmented, though third segment of endopod obscure. Coxa and basis unarmed. Exopod minute, 2.5 × 2.5 μm, with 1 seta. Endopod with first segment elongate with small knob on proximal outer corner and with few distal outer setules. Second segment triangular. Third segment with terminal claw 56 μm, 1 adjacent seta, and outer marginal setules.

Siphon (Fig. 11h) short, reaching only to bases of maxillipeds. Mandible (Fig. 11i) with long slender blade 160 μm, its tip dentate and expanded inwardly (Fig. 11j). Palp 1-segmented with long smooth seta, palp and seta together 164 μm. First maxilla (Fig. 12a) with both lobes bearing 4 setae, 2 setae on longer inner lobe barbed. Second maxilla (Fig. 12b) 2-segmented, first segment unarmed, second slender recurved segment clawlike, with faint indication of division midway, at that point bearing 1 seta and few very small spinules. Maxilliped (Fig. 12c) 5-segmented, first and second segments unarmed, third, fourth, and fifth segments with 1 seta each, claw 60 μm, with abruptly slender tip preceded by 1 minute inner spinule.

Ventral region between maxillipeds and first pair of legs not protuberant.

Legs 1–4 (Fig. 12d, e, g, i) biramous, with 3-segmented rami. Formula for armature as follows:

P_1 coxa 0-1 basis 1-I	exp I-0;	I-1;	III,I,4
	enp 0-1;	0-2;	1,2,3
P_2 coxa 0-1 basis 1-0	exp I-1;	I-1;	III,I,4
	enp 0-1;	0-2;	1,II,3
P_3 coxa 0-1 basis 1-0	exp I-1;	I-1;	III,I,4
	enp 0-1;	0-2;	1,II,3
P_4 coxa 0-1 basis 1-0	exp I-1;	I-1;	III,I,4
	enp 0-1;	0-2;	1,II,2

Inner coxal seta of leg 1 short, 13 μm, and smooth, that of leg 2 long and weakly plumose, that of leg 3 short as in leg 1, and that of leg 4 very short, 5 μm. Inner spine on basis of leg 1 44 μm, coarsely barbed along outer side and with setules along inner side (Fig. 12d). Legs 2–4 with few small spines on distal outer corner of coxa and on outer margin of basis. Inner margin of basis in leg 1 with row of small spines, in legs 2–4 this margin smooth. First segment of exopod of leg 1 with outer spine long and recurved, inner seta absent; in legs 2–4 this spine shorter and not recurved. Leg 2 in 1 female with endopod having formula 0-1; 0-2; 1,II,2 (Fig. 12f). Leg 3 in 1 female with endopod having 0-1; 0-2; 1,II,2 (Fig. 12h).

Leg 5 (Fig. 13a) with small subrectangular unornamented free segment 18 × 10.5 μm, its 3 setae from outer to inner 27, 25, and 8 μm. Adjacent dorsal seta 30 μm.

Leg 6 represented by 2 minute setae on genital area (Fig. 11d).

Color of living specimens in transmitted light opaque gray, eye red.

Male.—Body (Fig. 13b) with broad prosome slightly less orbicular than in female. Length 0.71 mm (0.65–0.75 mm) and greatest width 0.43 mm (0.42–0.45 mm), based on 6 specimens. Greatest dorsoventral thickness 0.18 mm. Epimera of segments bearing legs 1–4 serrate as in female. Ratio of length to width of prosome 1.12:1. Ratio of length of prosome to that of urosome 1.90:1.

Segment bearing leg 5 (Fig. 13c) 21 × 116 μm. Genital segment 104 × 150 μm, much wider than long. Length including leg 6 109 μm. Segment rounded laterally and bearing small scales. Three postgenital segments

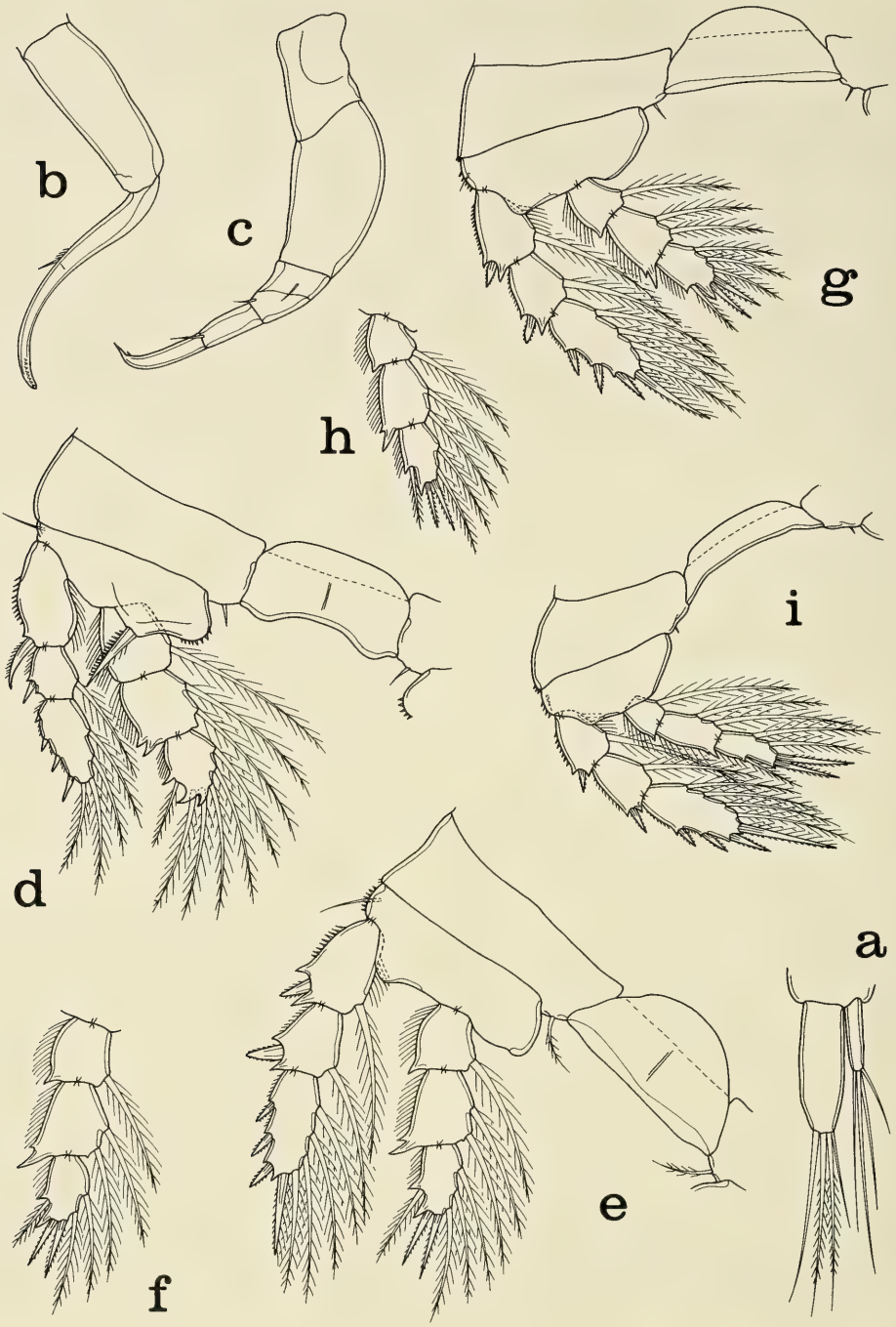


Fig. 12. *Hetairosyna laciniata,* female. a, First maxilla, posterior (scale E); b, Second maxilla, posterior (B); c, Maxilliped, posterior (B); d, Leg 1 and intercoxal plate, anterior (E); e, Leg 2 and intercoxal plate, anterior (E); f, Endopod of leg 2, anterior (E); g, Leg 3 and intercoxal plate, anterior (E); h, Endopod of leg 3, anterior (E); i, Leg 4 and intercoxal plate, anterior (E).

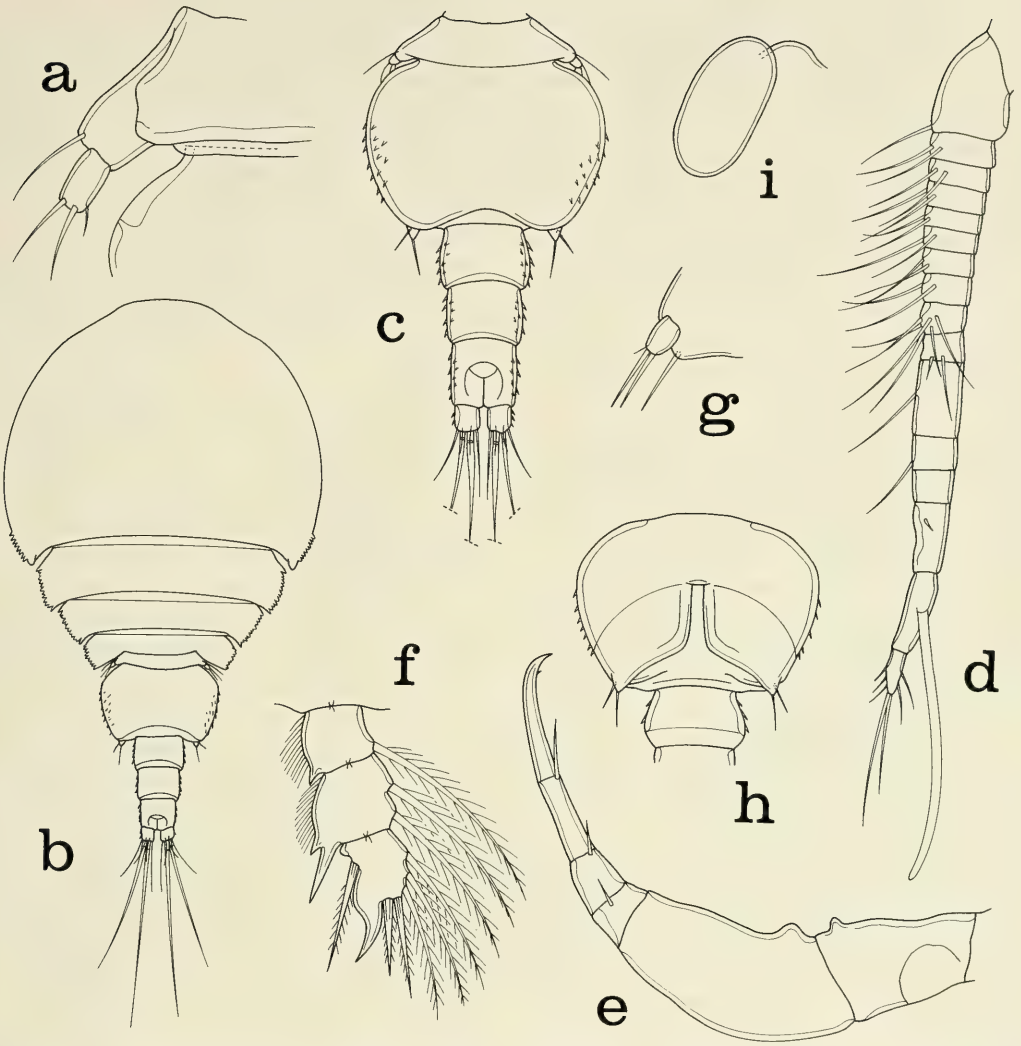


Fig. 13. *Hetairosyna laciniata.* Female: a, Leg 5, dorsal (scale C). Male: b, Dorsal (A); c, Urosome, dorsal (B); d, First antenna, anterodorsal (E); e, Maxilliped, posterior (E); f, Endopod of leg 3, anterior (C); g, Leg 5, ventral (F); h, Genital segment and first postgenital segment, ventral (B); i, Spermatophore, dorsal (E).

from anterior to posterior 34 × 65, 37 × 54, and 36 × 47 μm.

Caudal ramus similar to that of female but smaller, 16.5 × 18.5 μm, ratio 0.89:1.

Dorsal surface of body as in female; prosome tessellated as in that sex.

Rostral area as in female. First antenna (Fig. 13d) 280 μm long, 16-segmented. Lengths of segments: 23 (48 μm along anterior margin), 11, 8, 8, 8, 8, 9, 11, 10, 13, 30, 13, 11, 30, 36, and 17 μm, respectively. Armature: 1, 2, 2, 2, 2, 2, 2, 2, 6, 1 + 1 small spine, 1, 1, 0, 1, 0 + 1 aesthete, and 7. Setae hyaline and smooth. Second antenna, siphon, mandible, and first maxilla as in female. Maxilliped (Fig. 13e) similar to that of female but showing sexual dimorphism in having inner knob on both first and second segments. Postoral area like that of female.

Leg 3 with endopod showing sexual dimorphism (Fig. 13f), with spiniform process on second segment much longer than in female, third segment with distal outer process enlarged and sinuous and outer seta somewhat spiniform.

Leg 5 (Fig. 13g) with very small free segment 10 × 6 μm.

Leg 6 (Fig. 13h) posteroventral flap on genital segment bearing 2 small setae 26 and 17 μm.

Spermatophore (Fig. 13i) oval, 63 × 48 μm.

Color of living specimens as in female.

Etymology.—The specific name *laciniata,* Latin meaning fringed, refers to the finely serrated fringe on the epimera of the prosomal segments.

Remarks.—*Hetairosyna laciniata* may be recognized by the serrated fringe on the epimera of the prosomal segments in both sexes. In addition, the female of the new species shows several features that distinguish it from *H. terpna*: (1) the prosome is broader and more orbicular, (2) the female genital segment is as wide as long, (3) the seta on the palp of the mandible is smooth, (4) the second segment of the maxilliped is relatively shorter, (5) the inner coxal seta in legs 1–4 is short, and (6) the free segment of leg 5 is twice as long. In the male of *H. laciniata* the genital segment is much wider than in *H. terpna.*

Hetairosyna sororia, new species
Figs. 14, 15, 16

Type material.—10 ♀ from *Montipora ramosa* Bernard, in 2 m, north of Isle Maître, near Noumea, New Caledonia, 22°19′30″S, 166°24′35″E, 13 Jul 1971. Holotype (USNM 254436) and 7 paratypes (USNM 254437) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Remaining paratypes (dissected) in the collection of the author.

Other specimens.—From Madagascar, 1 ♀ from *Montipora sinensis* Bernard, in 1 m, Nosy Taolankena, near Nosy Bé, 15 Nov 1963; 1 ♀ from *Montipora* sp. cf. *M. stellata* Bernard, in 2 m, off Ampombilava, Nosy Bé, 26 Sep 1964.

From northeastern Australia: 2 ♀ from *Montipora verrilli* Vaughan, in 3 m, Mermaid Cove, Lizard Island, 14°39′50″S, 145°27′00″E, 27 Oct 1982.

From the Moluccas: 2 ♀ from *Montipora* sp. cf. *M. undata* Bernard, Poelau Parang, near Ceram, 03°17′00″S, 130°44′48″E, 23 May 1975.

Female.—Body (Fig. 14a) with broad prosome. Length 0.99 mm (0.94–1.01 mm) and greatest width 0.55 mm (0.50–0.61 mm), based on 10 specimens. Greatest dorsoventral thickness 0.30 mm. Epimera of segments bearing legs 1–3 pointed posteriorly, those of segment bearing leg 4 subtruncate. Ratio of length to width of prosome 1.26:1. Ratio of length of prosome to that of urosome 2.35:1.

Segment bearing leg 5 (Fig. 14b) 57 × 177 μm. Genital segment quadrate, 148 × 151 μm in dorsal view, with slightly convex sides. Genital areas situated dorsolaterally near middle of segment. Each genital area with 2 minute setae and spiniform process (Fig. 14b, c). Row of long strong setules on outer margin of segment posterior to genital areas. Two postgenital segments, first segment 62 × 92 μm, second segment 62 × 87 μm.

Caudal ramus (Fig. 14d) 29 × 36 μm in greatest dimensions, wider than long. Outer lateral seta, placed dorsally as in congeners, 107 μm, dorsal seta 65 μm, both smooth. Outermost terminal seta 165 μm, innermost terminal seta 195 μm, and 2 median terminal setae 330 μm (outer) and 380 μm (inner), swollen proximally, all with lateral setules.

Dorsal surface of prosome with extremely small scales. Urosome with more prominent scales (Fig. 14b) extending over dorsal and ventral surfaces (Fig. 14b,c) (all scales not illustrated). Caudal rami with few inner and outer scales (Fig. 14d).

Egg sac not seen.

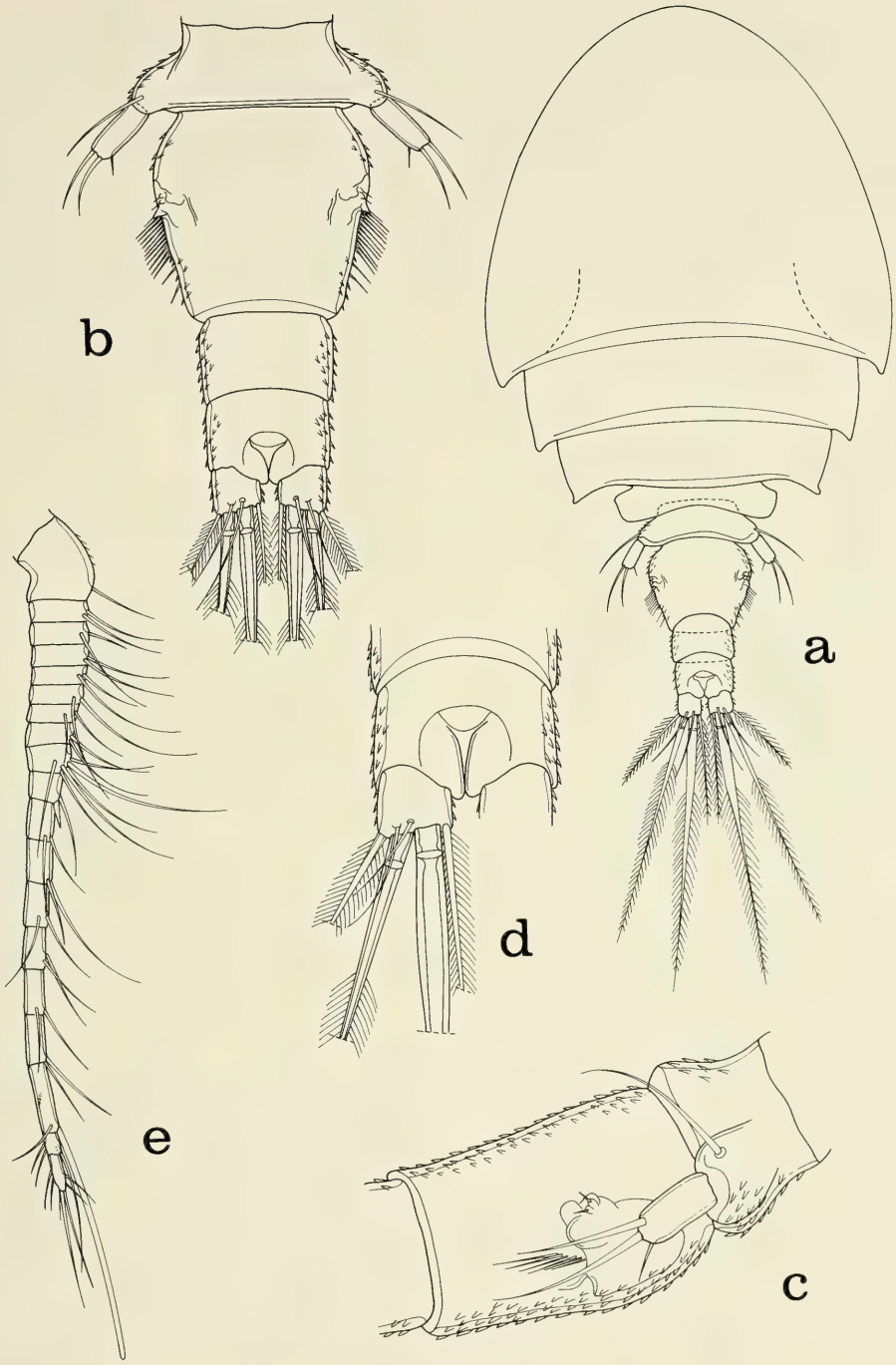


Fig. 14. *Hetairosyna sororia,* female. a, Dorsal (scale A); b, Urosome, dorsal (B); c, Segment bearing leg 5 and genital segment, lateral (B); d, Anal segment and caudal ramus, dorsal (E); e, First antenna, ventral (B). (In a–d scales not shown over entire surface.)

Rostral area weak, slightly protruding ventrally (Fig. 15b). First antenna (Fig. 14e) 460 μm long, 19-segmented. Lengths of segments: 26 (62 μm along anterior margin), 15.5, 13, 11, 11, 11, 11, 14, 15, 14, 31, 29, 31, 29, 31, 36, 43, 15, and 30 μm, respectively. Formula for armature: 1, 2, 2, 2, 2, 2, 2, 2, 6, 1 + 1 small spine, 2, 2, 2, 2, 2, 2, 2 + 1 aesthete, 3, and 7. All setae smooth. First segment with small spinules along convex margin.

Second antenna (Fig. 15a) 5-segmented, 352 μm long including claw. Coxa and basis unarmed. Exopod minute, 10 × 5 μm. Endopod with first segment elongate and unarmed, second segment with 1 small seta, and third segment with terminal claw 115 μm, 1 adjacent seta, and outer marginal row of setules.

Siphon (Fig. 15b, c) moderately slender, 180 μm long, reaching posteriorly beyond bases of maxillipeds. Mandible (Fig. 15d) with long slender blade 211 μm, its tip expanded outwardly as in *Hetairosyna terpna*; palp 1-segmented with long smooth terminal seta, palp and seta together approximately 200 μm long. First maxilla (Fig. 15e) with 2 unequal lobes, both with 4 setae, 2 of these setae on larger lobe with lateral setules; larger lobe with row of indistinct setules on anterior surface. Second maxilla (Fig. 15f) 2-segmented, first segment unarmed, second segment with minute seta proximal to middle of segment. Maxilliped (Fig. 15g) 5-segmented, armed as in *H. terpna,* claw 104 μm.

Ventral region between maxillipeds and first pair of legs protuberant (Fig. 15c).

Legs 1–4 (Figs. 15h, i, 16a, b) segmented as in congeners. Formula for armature as follows:

P_1 coxa 0-1 basis 1-I	exp I-1;	I-1;	II,I,4
	enp 0-1;	0-2;	1,5
P_2 coxa 0-1 basis 1-0	exp I-1;	I-1;	III,I,4
	enp 0-1;	0-2;	1,II,3
P_3 coxa 0-1 basis 1-0	exp I-1;	I-1;	III,I,4
	enp 0-1;	0-2;	1,II,3
P_4 coxa 0-1 basis 1-0	exp I-1;	I-1;	III,I,4
	enp 0-1;	0-2;	1,II,2

Inner spine on basis of leg 1 52 μm in length with long setules (Fig. 15h). Leg 1 with third segment of exopod having II,I,4, vestigial spine seen in congeners here absent. Inner coxal seta on leg 4 short, 16 μm.

Leg 5 (Fig. 16c) with free segment 47 × 23 μm, ornamented with few small outer spinules, bearing from outer to inner 3 setae 65, 55, and 18 μm. Adjacent dorsal seta 78 μm. All setae smooth.

Leg 6 represented by 2 minute setae on genital area (Fig. 14c). Color of living specimens in transmitted light transparent to opaque gray, eye red.

Male.—Unknown.

Etymology.—The specific name *sororia,* Latin meaning sisterly, alludes to the occurrence of this species along with two other species of *Hetairosyna.*

Remarks.—*Hetairosyna sororia* may be recognized by five features: (1) the siphon reaching posteriorly beyond the bases of the maxillipeds, (2) the strong setules on the lateral margins of the genital segment, (3) the lateral setules on the terminal setae of the caudal ramus, (4) the small spinules on the convex margin of the first segment of the first antenna, (5) the third segment of the exopod of leg 1 with II,I,4.

The three species of *Hetairosyna* may be differentiated as shown in Table 1.

Tychomyzon, new genus

Diagnosis.—Asterocheridae. Female: Two postgenital segments. Siphon relatively short. First antenna 18-segmented, with aesthete on segment 17. Second antenna with very small exopod, terminal segment of endopod with 1 claw and 1 seta. Mandible with 1-segmented palp bearing long seta. Leg 1 with first segment of endopod having inner seta. Leg 1 with inner coxal seta but this seta absent in legs 2–4. Third segment of endopod in legs 1–3 with formula 1,2,3, but in leg 4 with 1,2,1. Leg 4 with third segment of exopod having II,I,4. Leg 5 with minute free segment bearing 3 setae.

Male: Three postgenital segments. First antenna 16-segmented with aesthete on seg-

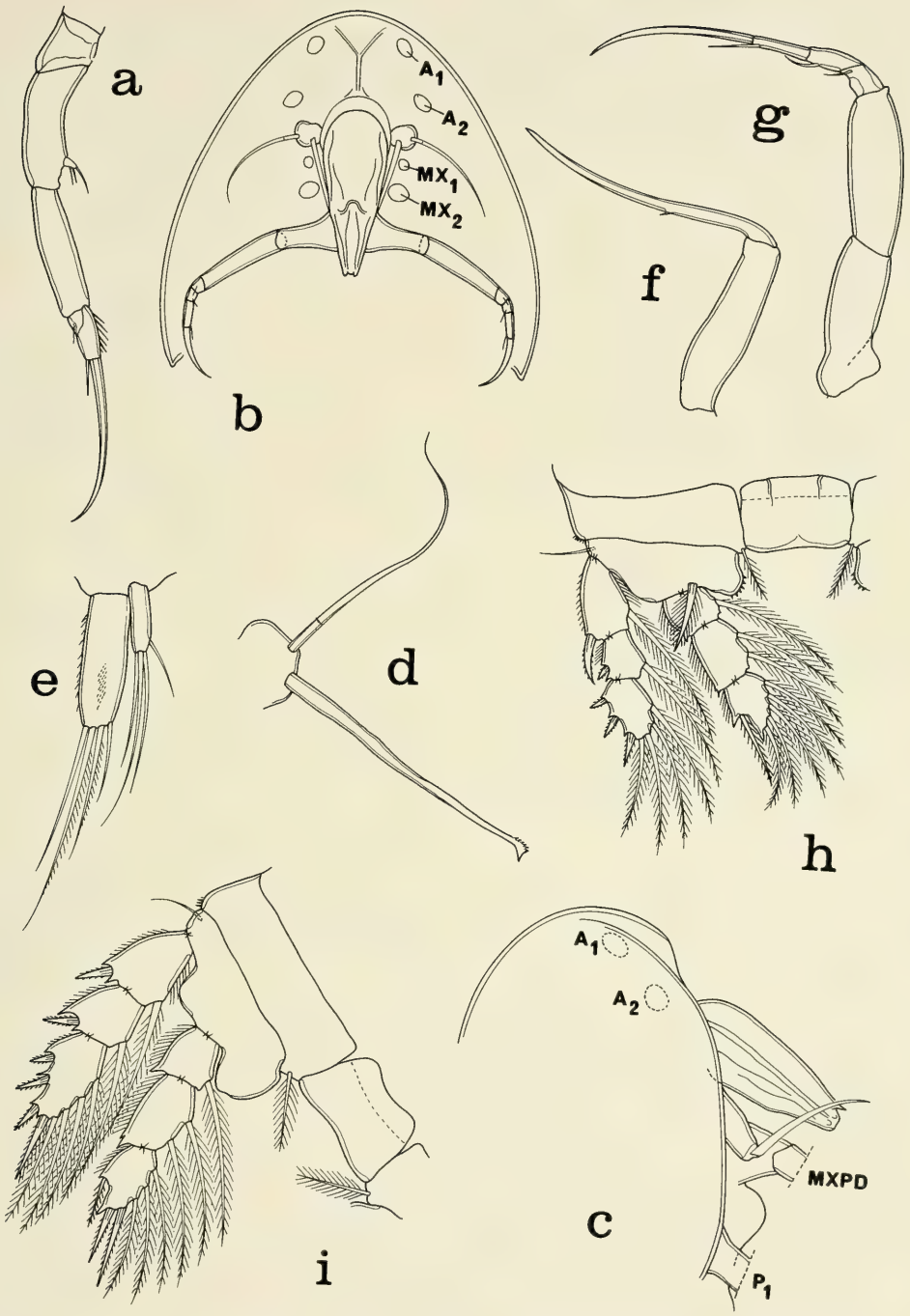


Fig. 15. *Hetairosyna sororia,* female. a, Second antenna, antero-outer (scale B); b, Cephalosome, ventral (A); c, Part of cephalosome, lateral (D); d, Mandible, anterior (B); e, First maxilla, posterior (E); f, Second maxilla, inner (B); g, Maxilliped, posterior (B); h, Leg 1 and intercoxal plate, anterior (B); i, Leg 2 and intercoxal plate, anterior (B).

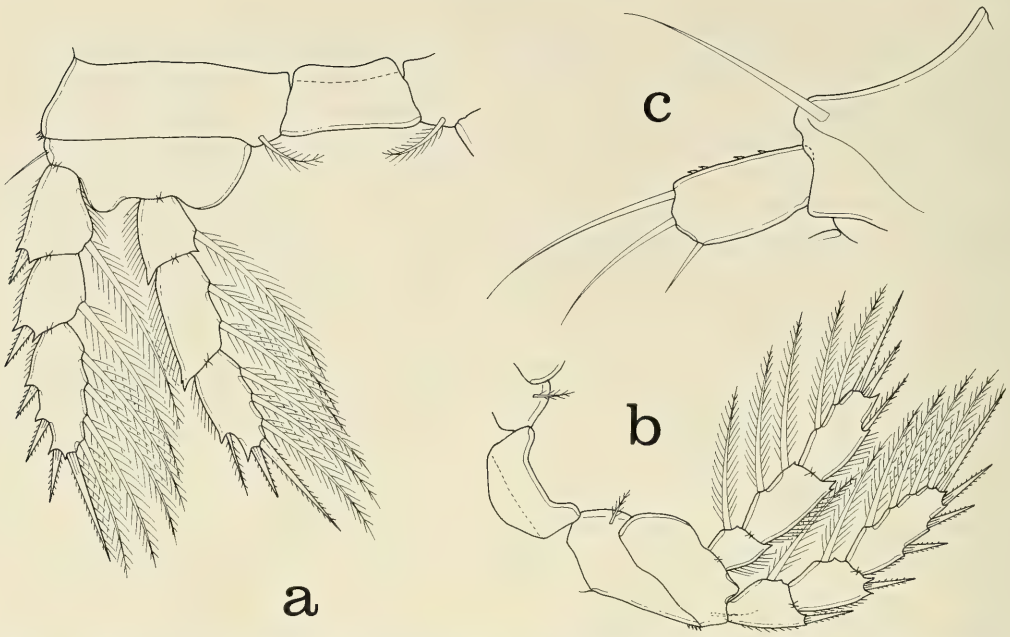


Fig. 16. *Hetairosyna sororia,* female. a, Leg 3 and intercoxal plate, anterior (scale B); b, Leg 4 and intercoxal plate, anterior (B); c, Leg 5, dorsal (C).

ment 15. Sexual dimorphism not expressed in legs 1–4.

Type species.—*Tychomyzon petalum,* new species.

Gender.—Neuter.

Etymology.—The generic name *Tychomyzon,* a combination of the Greek words *tyche,* good fortune, and *myzon,* used in the names of several asterocherid genera and derived from *myzao,* to suck.

Tychomyzon petalum, new species
Figs. 17, 18, 19

Type material.—7 ♀, 1 ♂ from *Montipora composita* Crossland, in 3 m, Mermaid Cove, Lizard Island, northeastern Austra-

Table 1.—Differentiation of the three species of *Hetairosyna,* based on females.

	H. terpna	*H. laciniata*	*H. sororia*
Prosome, ratio L/W	1.29:1	1.03:1	1.26:1
Prosomal epimera	smooth weakly rounded	fringed pointed	smooth pointed
Caudal ramus, terminal setae	with setules	smooth	with setules
Genital segment, dorsal view	153 × 127 μm	134 × 138 μm	148 × 151 μm
Genital segment, setules on sides	weak hairlike	weak hairlike	strong
Genital segment, dorsal surface	smooth	crescentic sculpturing	smooth
First antenna, anterior margin of first segment	smooth	smooth	with spinules
Siphon	reaches bases of maxillipeds	reaches bases of maxillipeds	reaches posterior to bases of maxillipeds
Leg 1 exopod, third segment	III,I,4	III,I,4	II,I,4
Leg 5, free segment	36 × 15.5 μm	18 × 10.5 μm	47 × 23 μm

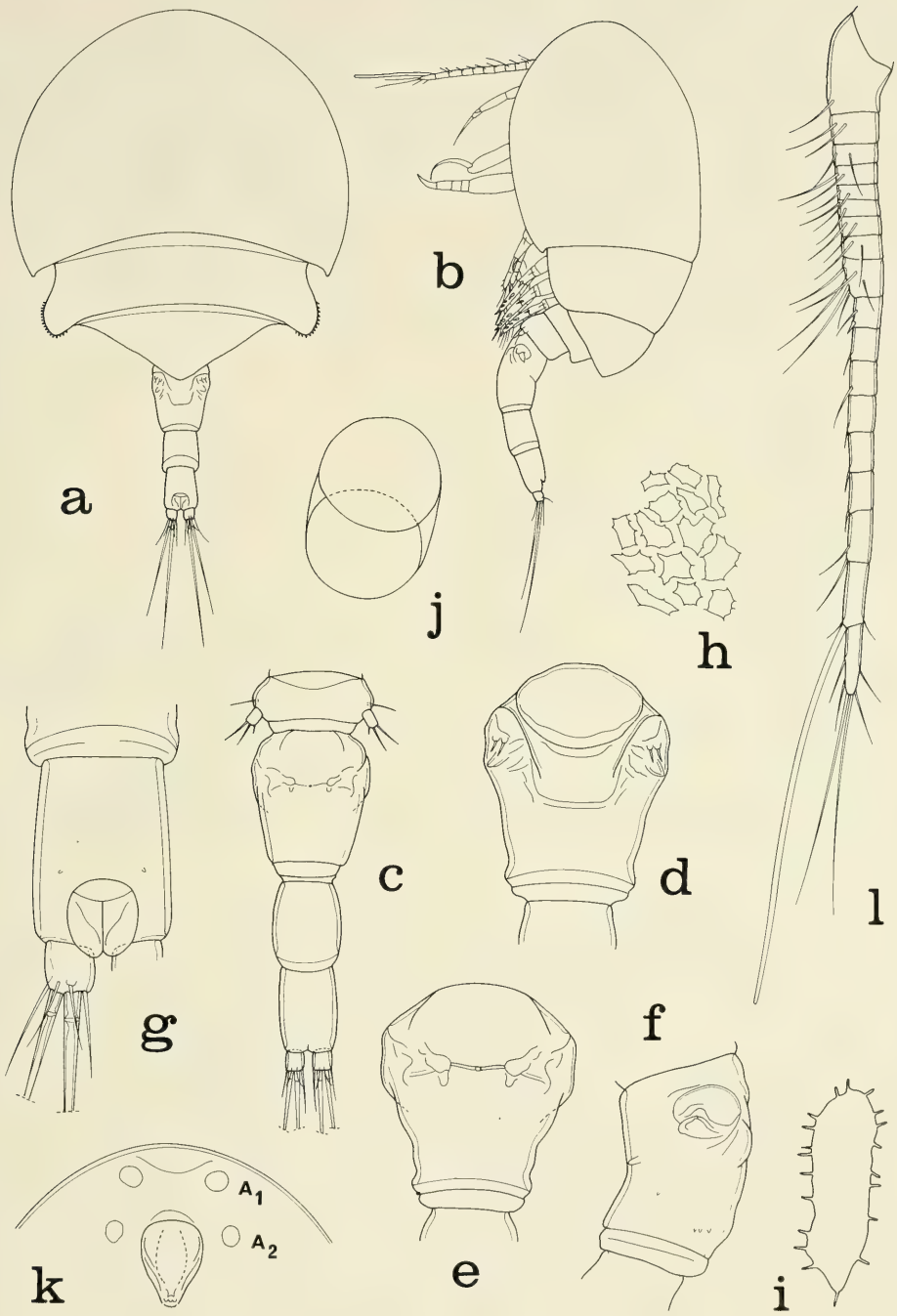


Fig. 17. *Tychomyzon petalum,* female. a, Dorsal (scale A); b, Lateral (A); c, Urosome, ventral (B); d, Genital segment, dorsal (D); e, Genital segment, ventral (D); f, Genital segment, lateral (D); g, Anal segment and caudal ramus, dorsal (C); h, Tesselations on dorsal surface of cephalosome, dorsal (E); i, Detail of tessellation on dorsal surface of cephalosome, dorsal (F); j, Egg sac, ventral (D); k, Rostral area and siphon, ventral (B); l, First antenna, posteroventral (C).

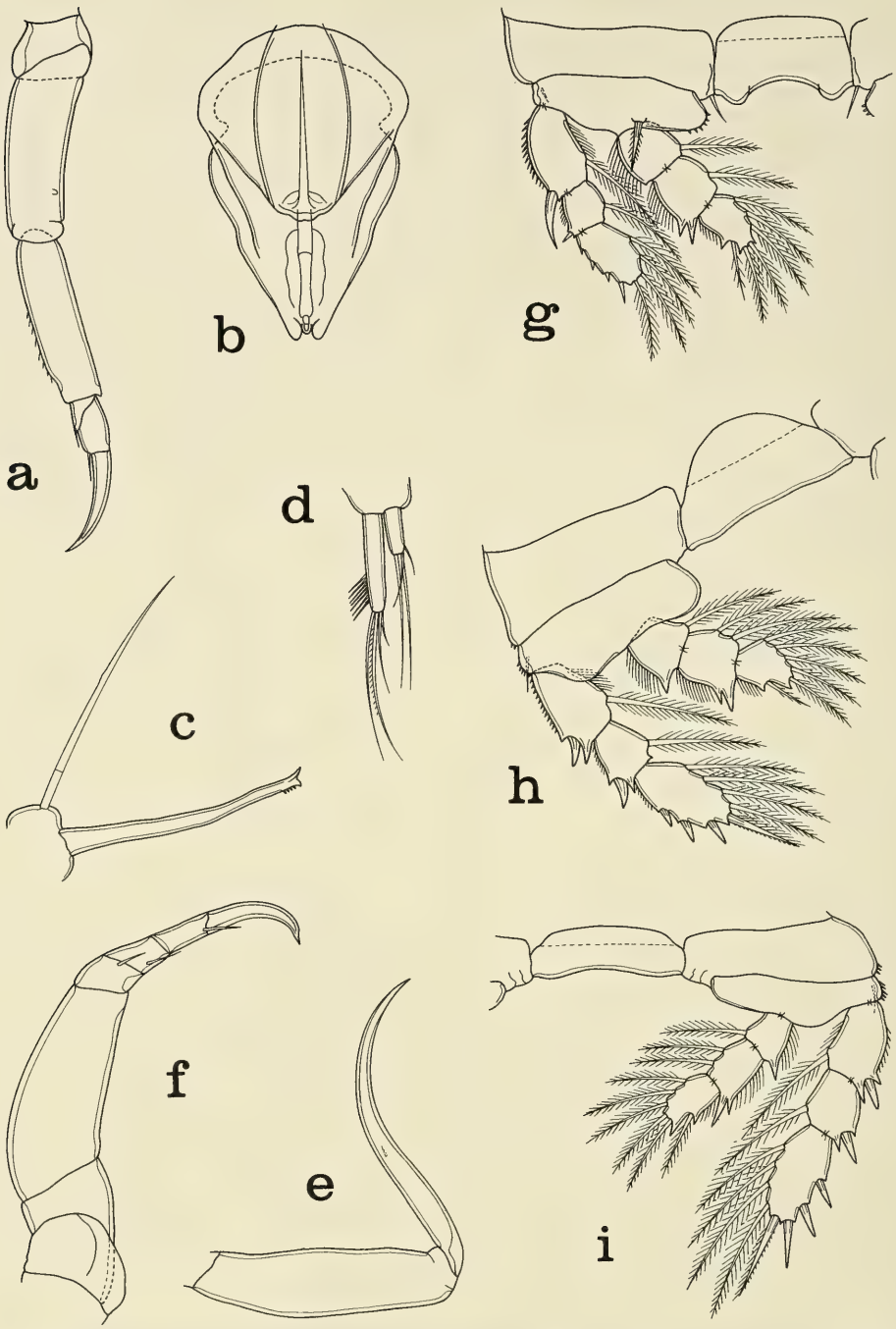


Fig. 18. *Tychomyzon petalum,* female: a, Second antenna, antero-outer (scale C); b, Siphon, dorsal (E); c, Mandible, anterior (E); d, First maxilla, anterior (E); e, Second maxilla, anterior (E); f, Maxilliped, posterior (E); g, Leg 1 and intercoxal plate, anterior (E); h, Leg 2 and intercoxal plate, anterior (E); i, Leg 3 and intercoxal plate, anterior (E).

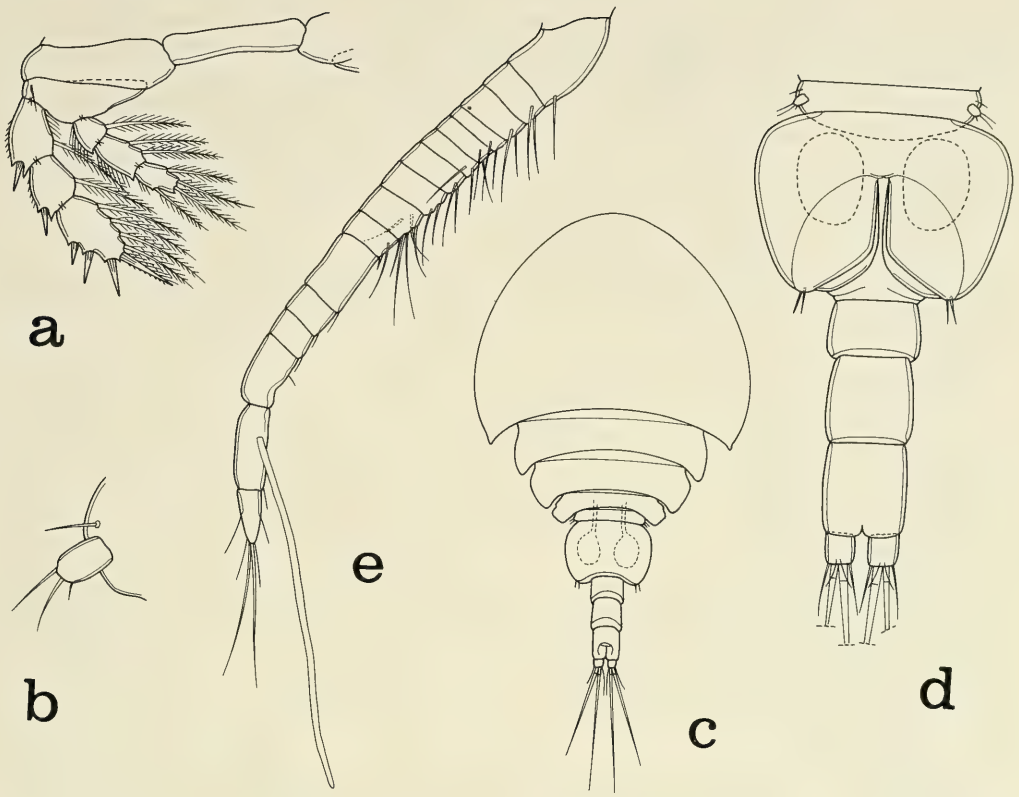


Fig. 19. *Tychomyzon petalum.* Female: a, Leg 4 and intercoxal plate, posterior (scale A); b, Leg 5, ventral (F). Male: c, Dorsal (A); d, Urosome, ventral (E); e, First antenna, anterodorsal (C).

lia, 14°39′50″S, 145°27′00″E, 27 Oct 1982. Holotype ♀ (USNM 254442), allotype (USNM 254441), and 4 paratype ♀ (USNM 254473) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Remaining paratypes (dissected) in the collection of the author.

Female.—Body (Fig. 17a, b) with broad prosome, segment bearing leg 4 hidden in dorsal view beneath more anterior segment (Fig. 17b). Length 0.74 mm (0.68–0.78 mm) and greatest width 0.51 mm (0.49–0.52 mm), based on 7 specimens. Greatest dorsoventral thickness 0.26 mm. Epimera of segment bearing leg 1 pointed, those of segment bearing leg 2 rounded and finely serrated. In dorsal view segment bearing leg 3 triangular and segment bearing leg 4 small, without expanded epimera. Ratio of length to width of prosome 1.19:1. Ratio of length of prosome to that of urosome 1.94:1.

Segment bearing leg 5 (Fig. 17c) 39 × 100 μm. Genital segment 109 × 88 μm, longer than wide, in dorsal view broadest in anterior half. Genital areas situated dorsolaterally, both bearing 2 small setae (Fig. 17d). Ventral surface with median opening of sperm duct (Fig. 17e, f).

Caudal ramus (Fig. 17g) small, subquadrate, 18 μm in outer length, 15 μm in inner length, and 18 μm wide. Outer lateral seta 20 μm (displaced dorsally), dorsal seta 22 μm, outermost terminal seta 38 μm, innermost terminal seta 30 μm, and 2 long median terminal setae 133 μm (outer) and 195 μm (inner). All setae smooth.

Dorsal surface of prosome with irregu-

Table 2.—*Montipora* in the Indo-Pacific and associated Copepoda. E = Enewetak Atoll, Marshall Islands, H = Hawaii, NC = New Caledonia, A = northeastern Australia, MOL = Moluccas, I = India, MAD = Madagascar, MAU = Mauritius.

Montipora ambigua Bernard	
Hetairosyna terpna, new species	E
Montipora caliculata (Dana)	
Euryte bellatula, new species	NC
Haplomolgus incolumis, new species	NC
Haplomolgus terpna, new species	NC
Montipora composita Crossland	
Haplomolgus montiporae Humes & Ho, 1968b	NC
Hetairosyna laciniata, new genus, new species	NC
Hetairosyna terpna, new species	A, NC
Odontomolgus forhani Humes, 1978 (present paper)	A, NC
Tychomyzon petalum, new genus, new species	A
Xarifia anopla Humes & Dojiri, 1982 (*in* Humes 1985)	A
Xarifia heteromeles Humes & Dojiri, 1982 (*in* Humes 1985)	A
Montipora compressa (Esper)	
Euryte bellatula, new species	MOL
Haplomolgus montiporae Humes & Ho, 1968b (*in* Humes 1978)	MOL
Hetairosyna terpna, new species	MOL
Odontomolgus forhani Humes, 1978	MOL
Montipora sp. cf. *M. efflorescens* Bernard	
Hetairosyna terpna, new species	NC
Montipora foliosa (Pallas)	
Indoclausia bacescui Sebastian & Pillai, 1974 (host reported as *M. foliacea,* but see Veron 1986:9–12)	I
Montipora lobulata Bernard	
Euryte bellatula, new species	NC
Haplomolgus montiporae Humes & Ho, 1968b (present paper)	NC
Hetairosyna laciniata, new species	NC
Hetairosyna terpna, new species	NC
Odontomolgus forhani Humes, 1978 (present paper)	NC
Montipora patula Verrill	
Hetairosyna terpna, new species	E
Montipora prolifera Brueggemann	
Euryte bellatula, new species	MOL
Hetairosyna terpna, new species	MOL
Odontomolgus forhani Humes, 1978	MOL
Montipora ramosa Bernard	
Euryte bellatula, new species	NC
Haplomolgus montiporae Humes & Ho, 1968b (present paper)	NC
Hetairosyna laciniata, new species	NC
Hetairosyna sororia, new species	NC
Hetairosyna terpna, new species	NC
Odontomolgus forhani Humes, 1978 (present paper)	NC
Xarifia pectinea Humes & Dojiri, 1982	NC
Xarifia temnura Humes & Ho, 1968a (*in* Humes & Dojiri 1982)	NC

Table 2.—Continued.

Montipora sinensis Bernard	
Haplomolgus montiporae Humes & Ho, 1968b	MAD
Hetairosyna laciniata, new species	MAD
Hetairosyna sororia, new species	MAD
Hetairosyna terpna, new species	MAD
Xarifia temnura Humes & Ho, 1968a	MAD
Montipora sp. cf. *M. stellata* Bernard	
Haplomolgus montiporae Humes & Ho, 1968b	MAD
Hetairosyna sororia, new species	MAD
Hetairosyna terpna, new species	MAD
Xarifia sp. (*in* Humes 1985)	MAD
Montipora sp. cf. *M. undata* Bernard	
Allopodion mirum Humes, 1978	MOL
Haplomolgus subdeficiens Humes, 1978	MOL
Hetairosyna sororia, new species	MOL
Kawanolus parangensis Humes, 1978	MOL
Odontomolgus forhani Humes, 1978 (present paper)	MOL
Xarifia anopla Humes & Dojiri, 1982	MOL
Xarifia heteromeles Humes & Dojiri, 1982	MOL
Xarifia syntoma Humes & Dojiri, 1982	MOL
Xarifia temnura Humes & Ho, 1968a (*in* Humes & Dojiri 1982)	MOL
Montipora verrilli Vaughan	
Alteuthellopsis corallina Humes, 1981 (*in* Humes 1984)	A
Euryte bellatula, new species	A
Haplomolgus montiporae Humes & Ho, 1968b (present paper)	A
Hetairosyna sororia, new species	A
Odontomolgus forhani Humes, 1978 (present paper)	A
Montipora verrucosa (Lamarck)	
Tegastes gemmeus Humes, 1984	H
Xarifia apertipes Humes & Dojiri, 1983	MAD
Montipora sp.	
Asteropontius corallophilus Stock, 1966	MAU
Haplomolgus montiporae Humes & Ho, 1968b (also *in* Humes & Stock 1973)	MAD
Hetairosyna terpna, new species	MAD
Xarifia anopla Humes & Dojiri, 1982	MAD
Xarifia extensa Humes & Dojiri, 1982	A, MAD

larly shaped tessellations having minute slender digitiform processes (Fig. 17h, i).

Egg sac (Fig. 17j) with 2 eggs, both approximately 130 × 117 μm.

Rostrum (Fig. 17k) small and inconspicuous. First antenna (Fig. 17l) 240 μm long, 18-segmented. Lengths of segments: 16 (32 μm along anterior margin), 11, 8, 8, 5, 5, 8, 10, 12, 10, 12, 12, 12, 12, 12, 16.5, 20, and 23 μm, respectively. Armature: 1, 2, 2, 2, 2, 2, 2, 2, 6, 1 + 1 small spine, 1, 1, 1, 1, 1, 2, 2 + 1 aesthete, and 6. All setae smooth and hyaline.

Second antenna (Fig. 18a) 5-segmented, 195 μm long. Coxa and basis unarmed. Exopod minute knob, 2 μm long, without visible setae. Endopod with elongate first segment bearing inner setules, short triangular

Table 3.—Copepoda associated with *Montipora* in the Indo-Pacific.

Allopodion mirum	*Montipora compressa*
Montipora sp. cf. *M. undata*	*Montipora* sp. cf. *M. efflorescens*
Alteuthellopsis corallina	*Montipora lobulata*
Montipora verrilli	*Montipora patula*
Asteropontius corallophilus	*Montipora prolifera*
Montipora sp.	*Montipora ramosa*
Euryte bellatula, new species	*Montipora sinensis*
Montipora caliculata	*Montipora* sp. cf. *M. stellata*
Montipora compressa	*Montipora* sp.
Montipora lobulata	*Odontomolgus forhani*
Montipora prolifera	*Montipora composita*
Montipora ramosa	*Montipora lobulata*
Montipora verrilli	*Montipora ramosa*
Haplomolgus incolumis, new species	*Montipora* sp. cf. *M. undata*
Montipora caliculata	*Montipora verrilli*
Haplomolgus montiporae	*Tegastes gemmeus*
Montipora composita	*Montipora verrucosa*
Montipora compressa	*Tychomyzon petalum*, new genus, new species
Montipora lobulata	*Montipora composita*
Montipora ramosa	*Xarifia anopla*
Montipora sp. cf. *M. stellata*	*Montipora composita*
Montipora sinensis	*Montipora* sp. cf. *M. undata*
Montipora verrilli	*Montipora* sp.
Montipora sp.	*Xarifia apertipes*
Haplomolgus subdeficiens	*Montipora verrucosa*
Montipora sp. cf. *M. undata*	*Xarifia extensa*
Hetairosyna laciniata, new genus, new species	*Montipora* sp.
Montipora composita	*Xarifia heteromeles*
Montipora lobulata	*Montipora composita*
Montipora ramosa	*Montipora* sp. cf. *M. undata*
Montipora sinensis	*Xarifia pectinea*
Hetairosyna sororia, new genus, new species	*Montipora ramosa*
Montipora ramosa	*Xarifia syntoma*
Montipora sinensis	*Montipora* sp. cf. *M. undata*
Montipora sp. cf. *M. undata*	*Xarifia temnura*
Montipora verrilli	*Montipora ramosa*
Hetairosyna terpna, new genus, new species	*Montipora sinensis*
Montipora ambigua	*Montipora* sp. cf. *M. undata*
Montipora caliculata	*Xarifia* sp.
Montipora composita	*Montipora* sp. cf. *M. stellata*

second segment with 1 seta, and third segment bearing terminally 1 claw 34 μm long and 1 seta.

Siphon (Figs. 17k, 18b) 150 μm long. Mandible (Fig. 18c) with long slender blade 109 μm, its tip inwardly dentate and expanded outwardly. Palp 1-segmented with long smooth seta, palp and seta together 117 μm long. First maxilla (Fig. 18d) with 2 unequal lobes, longer inner lobe with inner margin having setules and bearing 4 terminal setae, one of them unilaterally with setules; shorter outer lobe with 4 setae, one of them subterminal. Second maxilla (Fig. 18e) 2-segmented, first segment unarmed, second segment recurved with 1 minute seta midway on posterior surface. Maxilliped (Fig. 18f) 5-segmented, first 2 segments unarmed, last 3 segments with 1 seta each, terminal claw 47 μm with beaklike tip.

Legs 1–4 (Figs. 18g–i, 19a) biramous and 3-segmented. Formula for armature as follows:

P_1 coxa 0-1 basis 1-I	exp I-1;	I-1;	III,I,4
	enp 0-1;	0-1;	1,2,3
P_2 coxa 0-0 basis 1-0	exp I-1;	I-1;	III,I,4
	enp 0-1;	0-2;	1,2,3
P_3 coxa 0-0 basis 1-0	exp I-1;	I-1;	III,I,4
	enp 0-1;	0-2;	1,2,3
P_4 coxa 0-0 basis 1-0	exp I-1;	I-1;	III,I,4
	enp 0-1;	0-2;	1,2,1

Leg 1 with inner coxal seta, but this seta absent in legs 2–4. Basis of leg 1 having inner barbed spine 26 μm long, inner expansion of basis with row of small denticles on margin. Outer spine on first segment of exopod of leg 1 enlarged, recurved, 31 μm long. Leg 4 with third segment of endopod having 1,2,1.

Leg 5 (Figs. 17c, 19b) minute, free segment 13 × 9 μm, unornamented and inserted slightly ventrally. Free segment armed with 3 setae.

Leg 6 represented by 2 small setae on genital segment (Fig. 17d).

Color of living specimens in transmitted light opaque gray, eye red.

Male.—Body (Fig. 19c) with broad prosome. Length 0.51 mm, greatest width 0.40 mm, based on allotype. Segment bearing leg 4 not covered in dorsal view by segment bearing leg 3. Ratio of length to width of prosome 1:1. Ratio of length of prosome to that of urosome 1.53:1.

Segment bearing leg 5 (Fig. 19d) 31 × 90 μm. Genital segment 80 × 120 μm, wider than long, widest in anterior third. Three postgenital segments from anterior to posterior 28 × 46, 37 × 39, and 39 × 37 μm.

Caudal ramus like that of female but smaller, 13 × 13 μm.

Dorsal surface of prosome not tessellated as in female.

Rostrum similar to that of female. First antenna (Fig. 19e) 195 μm long, 16-segmented, slightly modified. Lengths of segments: 13 (33 μm along anterior margin), 10, 9, 4, 5, 6, 8, 9, 10, 10, 19, 9, 9, 21, 24, and 14 μm, respectively. Armature: 1, 2, 2, 2, 2, 2, 2, 2, 6, 1 + 1 small spine, 1, 1, 1, 1, 1 + 1 aesthete, and 6. Setae smooth and hyaline.

Second antenna, siphon, mandible, first maxilla, second maxilla, maxilliped, and legs 1–4 resembling those of female.

Leg 5 (Fig. 19d) with minute free segment approximately 8 × 6 μm.

Leg 6 (Fig. 19d) posteroventral flap on genital segment bearing 2 small setae.

Extruded spermatophore not seen.

Color as in female.

Etymology.—The specific name *petalum,* Greek *petalos,* broad, outspread, alludes to the unusually broad prosome.

Relatively few species of *Montipora* have been examined for copepod associates. The 15 species of *Montipora* recorded as hosts in Table 2 constitute less than half of the 38 species known from Australia listed by Veron (1986), and only a small fraction of the 211 nominal species. Ten species of *Montipora* have three or more species of copepod associates, with the greatest number being nine in the case of *Montipora* sp. cf. *M. undata* in the Moluccas. With 20 species of copepods already known to live with *Montipora* (Table 3), it seems certain that further studies will reveal many more copepods associated with this large and abundant coral genus.

Acknowledgments

I thank several individuals who have given much assistance and encouragement: Dr. Michel Angot, Director of the Centre ORSTOM de Nosy Bé, Madagascar, for making my work during more than two years at Nosy Bé pleasant and productive; Dr. Michel Pichon, James Cook University, Townsville, Australia, for arranging a diving trip to the Great Barrier Reef; Pierre Laboute, diver at the Centre ORSTOM de Nosy Bé, my companion on many SCUBA dives; Dr. Geoffrey A. Boxshall, British Museum (Natural

History) for helpful comments during the preparation of the manuscript; Dr. Thomas E. Bowman, National Museum of Natural History, Smithsonian Institution, for bibliographic information; and Dr. John H. Wells, Cornell University, for the identification of many of the corals.

Support from the following is gratefully acknowledged: the National Science Foundation (in Madagascar, 1963–1964, 1967; New Caledonia, 1971; the Moluccas, 1975; Hawaii and Australia, 1982) and the Eneweta k Marine Biological Laboratory (at Eneweta k Atoll, Marshall Islands, 1969).

Literature Cited

Boeck, A. 1859. Tvende nye parasitiske Krebsdyr, *Artotrogus orbicularis* og *Asterocheres liljeborgii*.—Forhandlinger i Videnskabs-Selskabet i Christiania 1859:171–182.

Burmeister, H. 1834. Beiträge zur Naturgeschichte der Rankenfüsser (Cirripedia). G. Reimer, Berlin. Pp. 1–59.

Dana, J. D. 1853. Crustacea. *In* United States Exploring Expedition during the years 1838–1842 under the command of Charles Wilkes 13(1):i–viii, 1–685, 13(2):686–1618.

Giesbrecht, W. 1899. Die Asterocheriden des Golfes von Neapel.—Fauna und Flora des Golfes von Neapel 25:i–vi, 1–217.

———. 1900. Mittheilungen über Copepoden. 12–14.—Mittheilungen aus der Zoologischen Station zu Neapel 14:39–82.

Humes, A. G. 1978. Lichomolgid copepods (Cyclopoda) associated with the coral genus *Montipora* in the Moluccas.—Publications of the Seto Marine Biological Laboratory 24:376–407.

———. 1981. Harpacticoid copepods associated with Cnidaria in the Indo-West Pacific.—Journal of Crustacean Biology 1:227–240.

———. 1984. Harpacticoid copepods associated with cnidarians in the tropical Pacific Ocean.—Zoologica Scripta 13:209–221.

———. 1985. A review of the Xarifiidae (Copepoda, Poecilostomatoida), parasites of scleractinian corals in the Indo-Pacific.–Bulletin of Marine Science 36:467–632.

———, & M. Dojiri. 1982. Xarifiidae (Copepoda) parasitic in Indo-Pacific scleractinian corals.—Beaufortia 32:139–228.

———, & ———. 1983. Copepoda (Xarifiidae) parasitic in scleractinian corals from the Indo-Pacific.–Journal of Natural History 17:257–307.

———, & B. W. Frost. 1964. New lichomolgid copepods (Cyclopoida) associated with alcyonarians and madreporarians in Madagascar.—Cahiers ORSTOM Océanographie, 1963, 6(série Nosy Bé II):131–212.

———, & R. U. Gooding. 1964. A method for studying the external anatomy of copepods.—Crustaceana 6:238–240.

———, and J.-S. Ho. 1968a. Xarifiid copepods (Cyclopoida) parasitic in corals in Madagascar.—Bulletin of the Museum of Comparative Zoology 136:415–460.

———, & ———. 1968b. Lichmolgid copepods (Cyclopoida) associated with corals in Madagascar.—Bulletin of the Museum of Comparative Zoology 136:353–413.

———, & J. H. Stock. 1972. Preliminary notes on a revision of the Lichomolgidae, cyclopoid copepods mainly associated with marine invertebrates.—Bulletin Zoologisch Museum, Universiteit van Amsterdam 2:121–133.

———, & ———. 1973. A revision of the Lichomolgidae, cyclopoid copepods mainly associated with marine invertebrates.—Smithsonian Contributions to Zoology 127:i–v, 1–368.

Kossmann, R. 1877. Entomostraca (l. Theil: Lichomolgidae). Pp. 1–24 *in* Zoologische Ergebnisse einer im Auftrage der Königlichen Academie der Wissenschaften zu Berlin aufgeführten Reise in die Küstensgebiete des Rothen Meeres, erste Hälfte, IV.

Philippi, A. 1843. Fernere Beobachtungen über die Copepoden des Mittlemeeres.—Archiv für Naturgeschichte 9:54–71.

Sars, G. O. 1913. An account of the Crustacea of Norway with short descriptions and figures of all the species. Pp. 1–32. *in* Vol. VI Copepoda Cyclopoida Parts I & II Oithonidae, Cyclopinidae, Cyclopinae (part). Bergen Museum, Alb. Cammermeyer's Forlag, Christiania, Norway.

Scott, T. 1912. The Entomostraca of the Scottish National Antarctic Expedition, 1902–1904.—Transactions of the Royal Society of Edinburgh 48:521–599.

Sebastian, M. J., & N. K. Pillai. 1974. Two new genera of clausiid copepods, *Indoclausia* and *Stockia*.—Crustaceana 26:80–88.

Sewell, R. B. S. 1949. The littoral and semi-parasitic Cyclopoida, the Monstrilloida and the Notodelphyoida. John Murray Expedition 1933–34, Scientific Reports, 13(2):17–199.

Stock, J. H. 1966. Cyclopoida siphonostoma from Mauritius (Crustacea, Copepoda).—Beaufortia 13:145–194.

———. 1975. Copepoda associated with West Indian Actiniaria and Corallimorpharia.—Studies on the Fauna of Curaçao and other Caribbean Islands 48:88–118.

———. 1987. Copepoda Siphonostomatoida asso-

ciated with West Indian hermatypic corals 1: associates of Scleractinia: Faviinae.—Bulletin of Marine Science 40:464–483.

———. 1989. Copepoda Siphonostomatoidea associated with West Indian hermatypic corals. 2.—Studies in honour of Dr. Pieter Wagenaar Hummelinck, Foundation for Scientific Research in Surinam and the Netherlands Antilles, Amsterdam 123:145–169.

Thompson, I. C., & A. Scott. 1903. Report on the Copepoda collected by Professor Herdman, at Ceylon, in 1902.—Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar, supplementary reports 7:227–307.

Thorell, T. 1859. Till kannedomen om vissa parasitiskt lefvande Entomostraceer.—Ofversift af Kongl. Vetenskaps-Akademiens Forhandlingar 16:333–362.

Ummerkutty, A. N. P. 1970. The genus *Euryte* Philippi (Copepoda, Cyclopoida) in Indian waters.—Records of the Zoological Survey of India, 1966 64:113–119.

Veron, J. E. N. 1986. Pp. i–xii, 1–664 *in* Corals of Australia and the Indo-Pacific. Angus & Robertson Publishers, North Ryde, New South Wales, Australia.

Vervoort, W. 1964. Free-living Copepoda from Ifaluk Atoll in the Caroline Islands with notes on related species.—United States National Museum Bulletin 236:i–ix, 1–431.

Boston University Marine Program, Marine Biological Laboratory, Woods Hole, Massachusetts 02543.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 138–146

PYCNOGONIDA OF THE WESTERN PACIFIC ISLANDS, IX. A SHALLOW-WATER GUAM SURVEY, 1984

C. Allan Child

Abstract.—Thirteen species of pycnogonids are reported from a 1984 survey of the shallow waters of Guam Island (13°30′N, 144°45′E) along with several juveniles and larvae which are left unidentified. One new species, *Eurycyde sertula,* is described and figured and its relationships with other species of the genus are discussed. The relationships and distribution of the other twelve species are listed and discussed.

The only previous report on Guam (Marianas Islands, 13°30′N, 144°45′E) pycnogonids (Child 1983) lists two species, both new, while concentrating mainly on the fauna of the western Caroline Islands at the Palau Islands. The present report contributes eleven additional species to the known Guam fauna, most of them previously known from nearby island groups. One species is described as new, *Eurycyde sertula,* and distributional data is given for all species.

These specimens were taken during most months of the 1984 year as the result of a shallow-water survey of the Island's macro- and microfauna. They were collected by Roy K. Kropp and others as part of PhD thesis work by Dr. Kropp. With the help of SCUBA, Kropp was able to sample the fauna of most of the Guam coast except for the most inaccessible areas. Specimens are deposited in the Pycnogonida collections of the National Museum of Natural History, Washington, D.C. (USNM).

Class Pycnogonida
Family Ammotheidae
Genus *Achelia* Hodge, 1864
Achelia assimilis (Haswell)

Ammothea assimilis Haswell, 1884:1026–1027, pl. LIV, figs. 5–9.

Achelia assimilis.—Child, 1990:312–313 [literature].

Material examined.—Calalan Bank, off Glass Breakwater, on dead branching coral in 12 m, 13 Sep 1984 (1 ♀ subadult, 1 larva).

Distribution.—This species has been taken at primarily southwestern Pacific localities and has recently been taken in Indonesia and the Philippines, all at shallow depths.

Remarks.—This is one of the most variable species in this genus whose species contain a wide variety of both intraspecific and interspecific differences. This female is fairly typical of those illustrated in previous publications.

Genus *Ammothella* Verrill, 1900
Ammothella tippula Child

Ammothella tippula Child, 1983;701–705, fig. 2; 1988a:7; 1988b:51.—Müller, 1990a: 67; 1990c:99; 1990d:106.

Material examined.—Agana Bay, 300 m N of boat basin channel, reef flat outer moat, rubble from 0.6 m, 5 Mar 1984 (1 ♂ with eggs); Piti Bay, Asan reef boulder area at margin SW of Camel Rock, from washings of *Halimeda* in 0.3 m, 10 Aug 1984 (1 ♀); Pago Bay, outer reef flat in front of marine laboratory, intertidal algal mat, 5 Oct 1984 (1 ♂); Luminao, reef flat opposite Family Beach, branching coralline algae in 1 m, 27 Oct 1984 (1 ♂, 1 Juv); Pago Bay, outer reef flat off marine lab, algal mat in 1–2 m, 2

Nov 1984 (1 ♀); Tumon Bay, reef front, dead branching coral in 11 m, 4 Nov 1984 (1 Juv); Apra Harbor, Family Beach, rubble in 1.2 m, 6 Dec 1984 (1 ♀).

Distribution.—The type locality for this species is Guam in shallow water (11 meters, the deepest known capture) and it has been taken once in the Sulu Sea, Philippines, also in shallow waters. These additional records add nothing to the known distribution of the species.

Remarks.—These specimens agree well with the type series and show very little or no variation in characters, particularly with the male.

Ammothella species indeterminate

Material examined.—Agana Bay, on rubble in 9 m, 3 Feb 1984 (1 Juv).

Remarks.—This specimen differs slightly in several characters from the predominant *A. tippula.* It is possibly *A. indica* Stock, but is too immature to be assigned to any species.

Genus *Eurycyde* Schioedte, 1857

Eurycyde sertula, new species

Fig. 1.

Material examined.—Ypan, branching coralline algae on algal ridge in 1 m, 23 Sep 1984 (1 ♀, holotype, USNM 234586).

Description.—Species moderately small for genus, leg span 5.1 mm. Trunk fully segmented, without median adornment. Lateral processes closely crowded, almost touching, not quite as long as their diameters, armed with small acute sharply pointed dorsodistal tubercles, the tallest on the anterior lateral process pair, shorter on each successive pair and tiny on posterior pair, tubercles without setae or spines. Ocular tubercle cylindrical, tapering distally, about 2.5 times longer than its diameter, armed with 5 large distal spines with setules arranged radially around tubercle tip which is terminally flat. Eyes large, filling distal half of ocular tubercle. Short neck constricted greatly just ventral to ocular tubercle which is situated just posterior to anterior rim of cephalic segment. Abdomen very broad, inflated, short, less than twice as long as its maximum diameter, armed with single encircling wreath of eleven long tubular spines bearing setules, spines situated slightly proximal to median circumference.

Proboscis typical of genus, basal stalk approximately 0.3 times length of distal proboscis segment which is more inflated proximally and slightly shorter than usual for genus.

Chelifores shorter than those of most species, first of scape segments equal in length to basal segment of proboscis, armed with single dorsodistal thick spine with setules. Second scape segment slightly shorter than first, more slender in diameter, armed with 8 thick spines matching that of first segment and 1–2 short distal setae. Chela vestigial, finger reduced to tiny knob, palm cylindrical, unarmed.

Palp typical for genus; of 10 segments. First two segments only as long as their diameters, third segment longest, armed with few short distal setae. Fourth segment very short, little longer than its diameter, armed with 2–3 short setae. Fifth segment slightly shorter than third, slightly inflated at midpoint, armed with long lateral spine and several distal short setae. Terminal five segments short, each armed with ventral field of short setae.

Oviger third segment longest, slightly longer than fourth which is armed with few short lateral setae. Fifth half length of fourth, armed with few lateral setae. Strigilis four segments armed with 2–3 short distal setae and endal denticulate spines in the formula 5: 4: 3: 5, with a small terminal claw shorter than terminal segment. Distal denticulate spine of terminal segment twice size of other spines, forming subchelate oviger terminus. Denticulate spines with four broad proximal lobes and two tiny distal lobes.

Legs moderately short, proximal segments broad, distal segments each with de-

creasing diameters. First coxae of anterior 3 pairs of legs with an anterodistal small conical tubercle armed with few tiny setae and much larger posterodistal tubercle as long as segment diameter, armed with two long inflated spines bearing setules and 1–2 short distal setae. First coxae of the posterior pair of legs have distal tubercles of similar size but without long inflated spines. Second coxae armed with 4–5 short lateral and ventral setae, third coxae with 2–3 short ventrodistal setae. Femorae the shortest of the major segments, armed with 1–2 short ventral setae and 5 long inflated dorsodistal and laterodistal spines bearing setules. First tibiae of smaller diameter, the longest major segments, armed with 3 long inflated dorsomedian spines with setules, 2 dorsodistal long inflated spines, the distal spine longest. Second tibiae similarly armed dorsally and with row of 4–5 ventral short setae. Tarsus subtriangular with 1–2 short ventral setae. Propodus only slightly curved, inflated, with 2 long dorsal setae and 7–8 short ventral sole spines. Claw half propodus length, slender, moderately curved, without auxiliaries.

Measurements (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes), 1.68; trunk width (across 2nd lateral processes), 1.28; proboscis length (distal segment), 1.39; abdomen length, 0.61, third leg, coxa 1, 0.12; coxa 2, 0.15; coxa 3, 0.12; femur, 0.34; tibia 1, 0.38; tibia 2, 0.35; tarsus, 0.09; propodus, 0.24; claw, 0.12.

Distribution.—The new species is only known from its type locality, the southeast coast of Guam at Ypan, on reef flat among intertidal coralline algae.

Etymology.—The species name is Latin (*sertula* is the diminutive of *serta,* meaning a garland or wreath) and refers to the single layered wreath-like circlet of long spines on the abdomen.

Remarks.—This third described species from western and mid-Pacific localities differs from the other two principally in the presence, absence, and armament of tubercles on the lateral processes and first coxae. Almost all known species of *Eurycyde,* the tropical species in particular, are very closely related and there exists only a narrow range of morphological characters for use in separating these species. One of the most reliable characters is that of tuberculation of the trunk extremities and leg coxae. Most known species have conspicuous dorsodistal tubercles on the first coxae and their size and armament are diagnostic.

Of the two known western Pacific species, *E. setosa* Child (1988a:8–10, fig.3) is the only one with lateral process tubercles which are very similar to those of *E. sertula.* The most recently described species (Müller 1990b:188–191, figs. 11–18), *E. longioculata,* lacks any form of lateral process tubercles, but has first coxae tubercles very similar to those of *E. setosa.* Both species have first coxae with a smaller anterodistal tubercle and a larger posterodistal tubercle, but those of *E. setosa* are clothed in short setae while those of *E. longioculata* have no conspicuous setae or spines. The coxae tubercles of *E. sertula* differ in having a much smaller anterodistal tubercle without setae and a much larger more robust posterodistal tubercle bearing pairs of long inflated spines with setules and 2–3 short setae, all distally placed. The posterior pair of first coxae have distal tubercles of almost the same size and neither bear long spines but only shorter setae.

Other major differences are in the length and spination of the ocular tubercle and abdomen. The new species has one of the shortest and broadest abdomens known in this genus and the eleven long spines are placed in a unique wreath-like fan around its circumference. The only other known species with a short abdomen bearing a circlet of long spines is *E. gorda* Child, but the abdomen is not nearly so inflated as that of the new species nor are the spines in a single flat plane as are those of *E. sertula.* The abdomen of *E. setosa* is unknown, having been broken off at its base before the unique type specimen was examined.

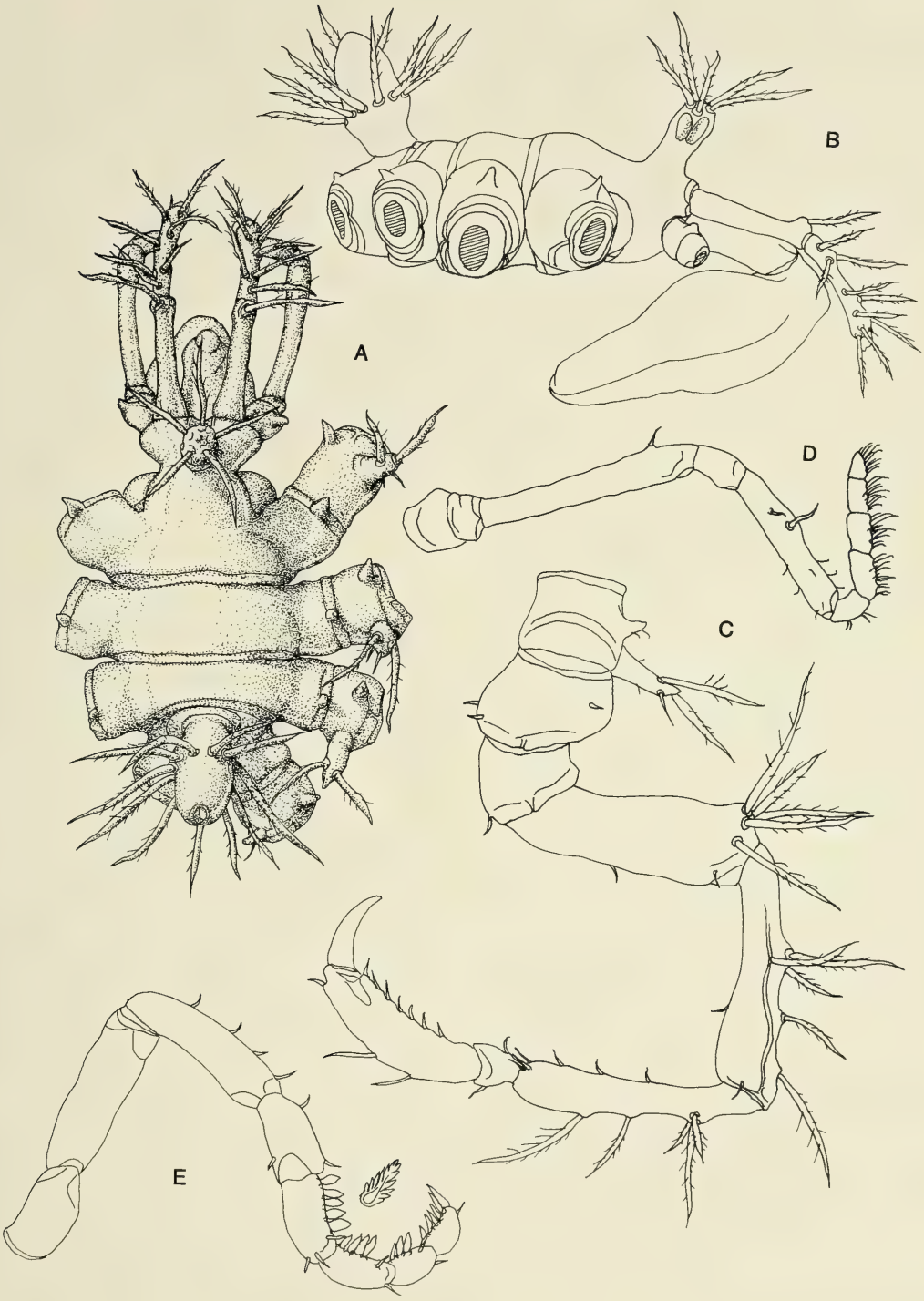


Fig. 1. *Eurycyde sertula,* holotype female: A, trunk, dorsal view; B, trunk, lateral view; C, third leg; D, palp; E, oviger with one denticulate spine, enlarged.

The ocular tubercle of the new species is very like that of *E. setosa* except that it is slightly shorter and the eyes are placed more distally in *E. sertula.* It is very different from the tall distally inflated ocular tubercle of *E. longioculata.* The count of long spines at the ocular tubercle tip differs for each of these species.

The legs, ovigers and palps of most *Eurycyde* species are remarkably alike except for interspecific differences in length versus diameter. Generally among the species of *Eurycyde,* (and among many other genera), the longer the appendage, the more slender are its segments. There are relatively minor differences in setae numbers but the numbers of long inflated spines bearing setules are more diagnostic as is their placement or absence. Their length varies among the species but those of the new species are somewhat shorter than usual while the long spines of *E. longioculata* appear to be longer than average.

The combination of lateral process, first coxae, abdomen and ocular tubercle characters discussed and compared above appear to be sufficient to designate this unique specimen as a new species.

Genus *Tanystylum* Miers, 1879
Tanystylum rehderi Child

Tanystylum rehderi Child, 1970:302–306, fig. 5; 1983:705; 1988b:53–54.—Müller, 1989:126, figs. 22–39.

Material examined.—Calalan Bank, off Glass Breakwater, reef front on dead branching coral in 12 m, 13 Sep 1984 (2 ♂, 1 ♀). Luminao, reef flat opposite Family Beach, on branching coralline algae in 1 m, 27 Oct 1984 (2 ♂ with eggs, 2 ♂, 3 ♀, 1 Juv). Tumon Bay reef front, on dead branched coral in 11 m, 7 Nov 1984 (1 larva, probably this species).

Distribution.—This species was described from specimens taken in Bora Bora and Moorea in the Society Islands, but was not found again in the former locality by Müller (1990b:185) in his survey. It was subsequently reported after its original description from the Palau Islands (Child 1983), on Aldabra Atoll (Child 1988b) in the Indian Ocean, and at the type locality on Mooréa (Müller 1989). The 11 meter depth given above is the deepest capture for this species which is usually taken in depths around 1 meter or less.

Remarks.—There is little to separate these specimens, particularly the large Luminao suite, from the type description. The large styliform proboscis shape of this species differs only slightly from those of several other species in this genus. What makes this species differ from the others are the height and shape of the tall rounded ocular tubercle, the abdomen with its basal swelling, and the male oviger with its wedge-shaped seventh oviger segment. The seventh oviger segment in *Tanystylum* either possesses or lacks a large lateral apophysis with long setae in the male, but that of this species is wedge-shaped rather than square or cylindrical as in most species bearing this character.

Genus *Anoplodactylus* Wilson, 1878
Anoplodactylus tenuicorpus, new combination

Anoplodactylus attenuatus Child, 1988a:12–14, fig. 5; 1988b:56, preoccupied by *Phoxichilidium attenuatum* Hodge, 1864.

Material examined.—Calalan Bank, off Glass Breakwater near Magundas, dead branching coral in 10 m, 16 Oct 1984 (1 ♀).

Distribution.—This species was described from the southern Philippines and subsequently found on Aldabra Atoll, Seychelles Islands, in the western Indian Ocean. This third report places it to the east of the type locality, at Guam, in the deepest capture thus far. It was previously taken in waters up to 6 meters deep.

Remarks.—No other species of this very

numerous genus is as attenuated as this species nor does any other have the serrated major heel spine in combination with this elongation of the trunk. The one species with a large serrated heel spine and a rather elongate trunk is *A. pectinus* Hedgpeth. Hedgpeth's species has shorter trunk segments, shorter lateral processes, a shorter proboscis, shorter oviger terminal segment, and in the male, has only a single cement gland opening per femur.

This species is easy to identify regardless of the sex of any specimen because it has the longest trunk segments of any known species. If the male is present, identification is made even easier by examination of the femorae which bear two cement gland pores.

Anoplodactylus chamorrus Child

Anoplodactylus chamorrus Child, 1983:705–707, fig. 3; 1988a:16; 1990:330–331.

Material examined.—Tumon Bay, reef flat off Fujita Hotel, rubble on outer reef platform in less than 1 m, 23 Mar 1984 (1 Juv). Agana Bay, 300 m N of boat basin channel, on rubble in 13 m, 25 Apr 1984 (1 ♀). Tanguisson Point, near bench margin, from intertidal algal turf, 17 May 1984 (1 ♀). Pugua Patch Reef (Double Reef), on rubble from 12 m, 3 Aug 1984 (1 Juv). Piti Bay, S of Camel Rock in boulder area at end of reef margin, from intertidal *Halimeda* washings, 10 Aug 1984 (1 ♂, 3 Juv). Sella Bay, from algae in 3 m, 14 Sep 1984 (1 Juv). Calalan Bank, off Glass Breakwater, from dead branching coral on reef front in 12 m, 13 Sep 1984 (1 ♀). Pago Bay, in reef front rock at 2.5 m, 18 Sep 1984 (2 ♀). Same locality, reef flat toward Pago River, in algae from intertidal reef pool, 21 Sep 1984 (1 ♀, 1 Juv). Luminao, reef flat near Magundas, on reef rubble in 1.3 m, 13 Oct 1984 (2 ♀). Calalan Bank, off Glass Breakwater near Magundas, dead coral rubble in 10 m, 16 Oct 1984 (1 Juv). Pago Bay, reef flat in front of marine laboratory, several samples from algal turf in 1–2 m, 17 and 20 Oct 1984 (2 ♀). Same location, from algal turf, after typhoon, 31 Oct and 2 Nov 1984 (1 ♂ with eggs, 2 ♂, 1 ♀, 2 Juv). Tumon Bay, reef front, from dead coral in 11 m, 7 Nov 1984 (1 Juv, 1 larva, possibly this species). Anae Island, halfway between island and shore, from algae in 3 m, 30 Nov 1984 (2 ♂, 3 ♀, 2 Juv).

Distribution.—From the wealth of specimens reported here, it would seem as though the longstanding "home" of this species is Guam. On the other hand, the species has been taken also at several localities in the southern Philippines and more recently on the Great Barrier Reef of Australia. Like many other species reported herein, the maximum depth records for this species are being extended by these new Guam records. The species had been found in depths of up to 3–4 meters and the Guam records now extend this known depth to 12 meters.

Remarks.—It is quite possible that some of the juvenile specimens listed here are not this species, but there is no other species known on Guam which bears the juvenile characters borne by these specimens. There are few species known with the combination of characters including the broad lateral 'collars' anterior to the first lateral processes, the closely crowded lateral processes separated only at their distal ends, the single tubular cement gland orifice per femur, the single major heel spine and very short propodal lamina, and an oviger with an extremely long first segment (almost twice as long as that of ovigers on other compact species). The juvenile specimens examined above have most of the characters listed except for cement glands and ovigers. The anterior collars and very crowded lateral processes are the most prominent characters in these juveniles.

Anoplodactylus glandulifer Stock

Anoplodactylus glandulifer Stock, 1954:80–84, fig. 36.—Child, 1983:273–274 [liter-

ature]; 1988b:58–59.—Nakamura & Child, 1988b:813.—Müller, 1990a:74.

Material examined.—Agana Bay, 300 m N of boat basin channel, on rubble in 9 m, 3 Feb 1984 (1 ♂).

Distribution.—This is a true Indo-West Pacific species, known from the Red Sea and Kenya to as far west as Samoa and as far south as the Great Barrier Reef, Australia, in many shallow-water habitats.

Anoplodactylus longiceps Stock

Anoplodactylus longicollis Williams, 1941: 36–38, figs. 2–5 [preoccup.]

Anoplodactylus longiceps Stock, 1951:16 [footnote]; 1954:83 [text]; 1956:97–98, figs. 14c–d.—Clark, 1963:56 [key].—Child, 1975:20, fig. 9f; 1990:331.

Material examined.—Calalan Bank, off Glass Breakwater, dead coral rubble in 10 m, 16 Oct 1984 (1 ♂).

Distribution.—This species is known from the east and west coasts of Australia and from the Kei Islands in eastern Indonesia in depths of 28–134 meters. This Guam specimen extends the known distribution of this species considerably into the Northern Hemisphere, but the specimen was taken within its known depths.

Remarks.—This species is very distinctive and is one of the relatively few known to have two cement gland orifices per femur (similar to those of *A. tenuicorpus,* listed elsewhere in this report). This Guam specimen differs very slightly from those figured in the literature. It has slightly shorter appendages with the tubercles of the femorae and first tibiae notably shorter, and the segments of the ovigers and chelifores are slightly shorter. The prominent propodal heel has two stout spines rather than the single spine borne by the type specimen, and the neck of the Guam specimen is swollen to accommodate the broader base of an ocular tubercle larger than that of the type. Other than these minor differences, the Guam specimen agrees very well with the type figures.

Anoplodactylus pycnosoma (Helfer)

Peritrachia pycnosoma Helfer, 1938:176–177, fig. 7.

Anoplodactylus pycnosoma.—Child, 1983: 708 [literature].—Nakamura & Child, 1983:50.—Hong & Kim, 1987:161.—Child, 1988a:20; 1988b:59.—Müller, 1990a:77; 1990c:100–102, figs. 7–13.

Material examined.—Pago Bay, reef flat near outer margin, from *Halimeda* washings in less than 1 m, 10 Feb 1984 (1 ♀). Tumon Bay, outer reef platform off Fujita Hotel, rubble in less than 1 m, 23 Mar 1984 (1 ♂). Pago Bay, reef flat in front of marine laboratory, algal turf in 1 m, 20 Oct 1984 (1 ♂, 1 ♀). Luminao, reef flat opposite Family Beach, branching coralline algae in 1 m, 27 Oct 1984 (2 ♀, 1 Juv). Adelup Point, on dead *Acropora* coral in 16 m, 20 Nov 1979 (1 ♂).

Distribution.—This often collected species is known from the African coast at Kenya and Tanzania to Japan, Korea, Philippines, Palau Islands, and with these records, Guam, all in very shallow waters.

Remarks.—The male has 5–8 femoral cement gland pores which serve as a stable recognition character in this otherwise rather plain species.

Family Endeididae Norman

The family name should have the entire suffix after the name instead of the suffix forming part of the body of the name as has been the case prior to this.

Genus *Endeis* Philippi, 1843

Endeis mollis (Carpenter)

Phoxichilus mollis Carpenter, 1904:182–183, figs. 1–7.

Endeis mollis.—Utinomi, 1971:327 [literature].—Stock, 1975a:1083–1085; 1975b: 76.—Nakamura & Child, 1983:41; 1988a:

664.—Child, 1988a:20–21.—Arnaud, 1988:52.

Material examined.—Tumon Bay, reef front, on dead finely branched coral in 11 m, 7 Nov 1984 (1 ♀ Juv, 1 Juv).

Distribution.—This is a pantropical shallow-water species.

Remarks.—This identification is based on the gut diverticula which in these specimens is relatively straight and without the conspicuous pockets or caeca of other Pacific species and these young specimens also lack the leg swellings and conspicuous leg spines of other species. It is probable that this set of characters means that these specimens are *E. mollis,* but an adult male from Guam is necessary to confirm this identification.

Family Callipallenidae Hilton
Genus *Callipallene* Flynn, 1929
Callipallene novaezealandiae (Thomson)

Pallene novae-zealandiae Thomson, 1884: 246–247, pl. 14, figs. 1–4.
Callipallene novaezealandiae.—Child, 1982: 277 [literature]; 1983:708; 1988a:21.—Nakamura & Child, 1988a:664.—Müller, 1990d:106.

Material examined.—Apra Harbor, Family Beach, rubble in 1 m, 20 Oct 1984 (1 ♂ with larvae, 1 ♀, 1 Juv). Luminao, reef flat opposite Family Beach, on branching coralline algae in 1 m, 27 Oct 1984 (1 Juv). Tumon Bay, reef front, on dead branching coral in 11 m, 7 Nov 1984 (1 larva, probably this species).

Distribution.—This species occupies many Indo-West Pacific localities from east Africa through Australia and New Zealand to Japan from intertidal depths to about 275 meters.

Genus *Seguapallene* Pushkin, 1975
Seguapallene micronesica Child

Seguapallene micronesica Child, 1983:709–711, fig. 4; 1990:324 [text].

Material examined.—Tumon Bay, reef front, on dead branching coral in 11 m, 7 Nov 1984 (1 ♂).

Distribution.—This species was described from the Palau Islands in intertidal depth. This additional record extends the Pacific distribution of this species to the northeast and, like many species in this report, extends its maximum capture depth to 11 meters from shallower depths.

Remarks.—There are only three species in Pushkin's genus and this species has more similarities to the other known tropical form, *S. crassa* Child (1990:321–324, fig. 4), than to Pushkin's Subantarctic type. *Seguapallene micronesica* has separated lateral processes (crowded and touching in *S. crassa*), a very short main propodal claw (longer and more typical in *crassa*), well separated triangular chelae teeth (block-like and touching in *crassa*), and moderately long and slender leg segments (shorter and robust in *crassa*).

The single character separating this genus from the much more numerous genus *Callipallene* is the presence of a large terminal oviger claw which may or may not have serrations or denticulations on its endal surface.

Family Nymphonidae Wilson
Genus *Nymphon* Fabricius, 1794
Nymphon diabolus Child

Nymphon diabolus Child, 1988a:23–25, fig. 10; 1988b:75.—Nakamura & Child, 1988a:668.

Material examined.—Agana Bay, 300 m N of boat basin channel, reef front, on dead branching coral in 9–10 m, 11 Sep 1984 (1 ♂ with eggs). Calalan Bank, off Glass Breakwater near Magundas, dead branching coral in 10 m, 16 Oct 1984 (2 ♀).

Distribution.—This species was recently reported from two localities in the southern Philippines, taken in 1–6 meters. These records extend its known distribution to the east at Guam and into slightly deeper water.

Remarks.—This small *Nymphon* is easily distinguished from the growing list of shallow-water species in the tropics by the reduced size of everything anterior to the neck in relation to the remainder of the trunk which is noticeably larger. The species is otherwise undistinguished, but with both proboscis and chelifores shorter than the length of the first or cephalic segment, the species should be easily separable. It also has a pair of conspicuous lateral tubercles on the ocular tubercle apex.

Acknowledgments

My warmest thanks are extended to Roy K. Kropp for the privilege of examining this collection, for his excellent collecting notes, and for his enthusiasm in discussing the arts of collecting along the varied and sometimes precipitous coasts of Guam Island. I am grateful also to his several diving partners for their specimen additions.

Literature Cited

For the literature published prior to 1978, see the complete bibliography published by Fry & Stock 1978.

Arnaud, F. 1988. Les Pycnogonides (Chelicerata) de Mediterranee: distribution, ecologique, bathymetrique et biogeographie. Mesogee, Bulletin du Museum D'Histoire Naturelle de Marseille 47(1987):37–58.

Child, C. A. 1982. Pycnogonida of the western Pacific islands, I. The Marshall Islands.—Proceedings of the Biological Society of Washington 95:270–281.

———. 1983. Pycnogonida of the western Pacific islands, II. Guam and the Palau Islands.—Proceedings of the Biological Society of Washington 96:698–714.

———. 1988a. Pycnogonida of the western Pacific islands III. Recent Smithsonian-Philippine expeditions.—Smithsonian Contributions to Zoology 468:1–32.

———. 1988b. Pycnogonida from Aldabra Atoll. Pp. 45–78 *in* B. Kensley, ed., Results of recent research on Aldabra Atoll, Indian Ocean. Bulletin of the Biological Society of Washington 8:1–138.

———. 1990. Pycnogonida of the western Pacific islands, VIII. Recent collections from islands of the Great Barrier Reef, Australia.—Proceedings of the Biological Society of Washington 103: 311–335.

Fry, W. G., & J. H. Stock. 1978. A Pycnogonid bibliography. *In* Sea spiders (Pycnogonida).—Zoological Journal of the Linnean Society of London 63(1+2):197–238.

Hong, J.-S., & I.-H. Kim. 1987. Korean pycnogonids chiefly based on the collections of the Korea Ocean Research and Development Institute.—The Korean Journal of Systematic Zoology 3: 137–164.

Müller, H.-G. 1989. Shallow-water Pycnogonida from coral reefs at Moorea, Society Islands, with description of *Rhynchothorax tiahurensis* n. sp.—Bonner Zoologische Beitrage 40:123–139.

———. 1990a. Shallow-water Pycnogonida from Kenya and Sri Lanka, with descriptions of three new species.—Bonner Zoologische Beitrage 41: 63–79.

———. 1990b. Flachwasser-Pantopoden von Bora-Bora, Gesellsc haftsinseln, S-Pazifik, mit zwei Neubeschreibungen (Pantopoda).—Senckenbergiana biologica 70(1989):185–201.

———. 1990c. Pycnogonida from Coral Reefs at Réunion Island, Southern Indian Ocean.—Zoologische Abhandlungen Staatliches Museum für Tierkunde Dresden 45:97–102.

———. 1990d. On some Indo-West-Pacific Pycnogonida from the Zoologisk Museum, Copenhagen.—Zoologische Abhandlungen Staatliches Museum für Tierkunde Dresden 45:103–110.

Nakamura, K., & C. A. Child. 1983. Shallow-water Pycnogonida from the Izu Peninsula, Japan.—Smithsonian Contributions to Zoology 386:1–71.

———. 1988a. Pycnogonida of the western Pacific islands, IV. On some species from the Ryukyu Islands.—Proceedings of the Biological Society of Washington 101:662–670.

———. 1988b. Pycnogonida of the western Pacific islands, V. A Collection by the *Kakuyo Maru* from Samoa.—Proceedings of the Biological Society of Washington 101:809–816.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 147–158

TRICHOBRANCHIDAE (POLYCHAETA) FROM SHALLOW WARM WATER AREAS IN THE WESTERN ATLANTIC OCEAN

Vivianne Solis-Weiss, Kristian Fauchald and Arno Blankensteyn

Abstract.—Three new species of *Terebellides* from shallow tropical waters are described: *T. parvus* from Belize, *T. carmenensis* from Mexico, and *T. lanai* from Brazil. *Terebellides klemani* and *T. anguicomus* are redescribed and recognized as distinct.

The most common trichobranchids in shallow water in Belize and the Mexican shallow-water lagoons along the Gulf of Mexico belong to a species group which also includes *Terebellides klemani* Kinberg, 1867 and *T. anguicomus* Müller, 1858. *Terebellides klemani* has been considered a synonym of *T. anguicomus* (see Hessle, 1917). After examining specimens from Belize and closely similar specimens from Mexico, the types of *T. klemani* and specimens collected near the type areas of both previously named species, we believe that we can recognize a series of similar, but distinct, species all of which would have been subsumed under Hessle's concept of *T. anguicomus*.

Our study parallels the analysis of the "cosmopolitan species" *T. stroemi* Sars, 1835 published by Williams (1984). Williams used several characters rarely noted in descriptions of trichobranchids to subdivide *Terebellides stroemi* s. l.; our observations generally support her conclusions about the importance of characters not previously used to delimit species.

Williams did examine specimens from Central America and Northern South America, but was not able to assign them to species other than to note that they did not belong in the species-complex she was analyzing. Her specimens from the region of interest in this study appear to be closely similar to *T. klemani* and to other species described in this study.

Materials and methods.—Material for this study came from several sources:

1) Belize: More than 550 specimens collected by the second author and B. F. Kensley (1979–1981) as part of the SWAMP (Smithsonian Western Atlantic Mangrove program) directed by Klaus Rützler. The first 10 cores were taken with a corer of 25 cm diameter; the rest with a 10.4 cm diameter corer. All were taken to a substrate depth of approximately 10 cm. Details of the collection, screening and preservation methods can be found in Solis-Weiss & Fauchald (1989).

Station list.—West Bay, Twin Cays, Belize, 10–50 cm water depth; root mat of *Rhizophora mangle,* covered with *Caulerpa verticillata.* Core numbers: M1–M3; M5–M13; M16; M20; M24–M28; M31–M36; M39–M42; M45–M47; M51–M55; M58–M60; M63; M68–M69; M71; M88; M90; M94–M96; M100–M101; M107; M133; M139–M148.

West side of middle island, Blue Ground Range, Belize, 10–50 cm water depth, root mat of *Rhizophora mangle* covered with *Caulerpa verticillata.* Core numbers: M65; M75; M80–M81; M84; M150.

2) Mexico: Specimens from Laguna de Terminos, Campeche collected by the senior author and P. Hernandez-Alcantara (1983–1984) as part of the collaborative project UNAM-CONACYT-QCMABFR-001698. Specimens in sediments associated with *R. mangle,* as in Belize, and at similar water depths. Algal mat was absent. The samples were taken with a 25 cm corer to a substrate depth of 20 cm. Details of sam-

pling methods, localities, screening and preservation were described elsewhere (Hernández-Alcantara 1985).

3) Brazil: This material was kindly sent us by Dr. Paulo da Cunha Lana and collected either by him in Baia de Paranagua (1981–1986), or during "Operacao Sueste" (1982–1983) on the R/V *Almirante Saldanha*; it represents part of the material used by the third author during his academic studies. Sampling localities are given in the text.

4) Type material of *Terebellides klemani* housed in Riksmuseet, Stockholm, Sweden.

For examination of gland patterns, the specimens were stained with a methylene blue solution and rinsed with 70% ethanol to remove excessive staining, following methods suggested by Banse (1970).

Measurements were made to the nearest $\frac{1}{10}$ mm. All length measures were taken from the posterior edge of the prostomium; the flattened, foliose prostomium varies a great deal in length and shape with fixation as do the tentacles.

The morphological terminology was derived from Fauchald (1977) and Williams (1984).

Abbreviations: Capital M in the station data refers to the location of the samples in the mangroves; specimens from these samples are deposited as indicated in the text. RM-Naturhistoriska Riksmuseet, Stockholm, Sweden; USNM indicates samples cataloged in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Systematic Section

Family Trichobranchidae Malmgren, 1866
Genus *Terebellides* Sars, 1835

Key to Species of *Terebellides* of the *anguicomus* Group

1. 17 thoracic setigers, first uncini on setiger 5 ..... *T. anguicomus*
– 18 thoracic setigers, first uncini on setiger 6 2
2. Anterior dorsum with distinct hump ..... *T. carmenensis*
– Anterior dorsum smoothly curved 3
3. 20–26 abdominal setigers present ..... *T. parvus*
– At least 30 abdominal setigers present 4
4. Branchiae free almost to base .... *T. klemani*
– Branchiae fused for most of their length ..... *T. lanai*

Terebellides klemani Kinberg, 1867
Fig. 1a–f

Terebellides klemani Kinberg, 1867:346.—Hartman, 1948:14.

Terebellides anguicomus.—Hessle, 1917: 141, fig. 33a–c (in part, not *T. anguicomus* Müller, 1858, see below).

Material examined.—Three syntypes, RM 975(1) and 976(2), *Eugenie* Expedition sta. 180. Atlantic Ocean: 22°30′S, 40°55′W; 36–73 m.

Comments on material examined.—The three available specimens are all in poor condition. One (here called 976b) is posteriorly incomplete and has a damaged prostomium and branchiae. The other two specimens are complete. All three specimens have crystals imbedded in the epidermis making observation of some structures very difficult. Staining with methyl blue failed to improve the resolution of such features as the numbers of hooks present. The description is based on the larger of the two complete specimens (976a) with comments on the other specimens where appropriate.

Description.—Syntype 976a with 18 thoracic and 32 abdominal setigers; length 23 mm, measured from the posterior edge of the prostomium. Syntype 976b posteriorly incomplete, with 18 thoracic and 37 abdominal setigers; length 35 mm. Syntype 975 with 18 thoracic and 30 abdominal setigers; length 9.6 mm.

Prostomium large and folded; many tentacles of two different widths. Tentacles of other two specimens all similar in width. Elongated nephridial papillae present dorsally on either side of base of branchial stalk.

Branchiae appearing 5-lobed; both superior lobes projecting forward. Branchial lobes free almost to the base of the stalk. All lobes similar in size and width. In syntype 975 inferior lobes conspicuously slenderer than other lobes and fused for ⅓ of their length. Posterior edge of each branchial lamella with slender papillar projections in a single row (Fig. 1a).

First two parapodia located slightly dorsal to next following parapodia (Fig. 1a). Lateral lappets with rounded ear-like projections in setiger 1; projections increasingly inconspicuous in setigers 2–3. Abdominal neuropodial tori fringed by single rows of uncini. Posterior segments crowded making neuropodia increasingly crowded towards posterior end.

Pygidium conical; anus terminal; surrounded by several blunt papillae.

Notopodial setae of setiger 1 few in number and short; more numerous and well developed from setiger 2 on. All notosetae long, distally pointed, delicately limbate and capillary. Four large, distally pointed, curved and retractile acicular spines present in neuropodium 6 (Fig. 1b); tips easily broken. Neuropodia with single rows of curved uncini with large main fangs and numerous secondary teeth in setigers 7–18 (Fig. 1c, d). Number of uncini per row 10–14 in all thoracic neuropodia in all three specimens. Each abdominal neuropodium with a single row of about 35 avicular multidentate uncini (Fig. 1e, f).

No tubes present in material.

Methylene blue staining pattern transverse stripes on 11 anterior setigers in syntype 975; absent in syntypes 976a and 976b.

Discussion.—Hartman (1948) examined these specimens and apparently recognized them as the types of Kinberg's species even if she did not report on the species. The relationship between this species and the similar *T. anguicomus* is discussed below. The species is currently known only through the original record by Kinberg (1867) from the Brazilian coast, but as indicated below, at least some of the records of *T. anguicomus* may belong to this species.

Terebellides anguicomus Müller, 1858
Fig. 1g–i

Terebellides anguicomus Müller, 1858:218, pl. 7, figs. 22–25.—Hessle, 1917:141, fig. 33a–c (in part).

Material examined.—Sta. 6290, Operacao Sueste II, R/V *Almirante Saldanha,* 24°06′0″S, 46°10′0″W, col. Operacao Sueste II, 31 May 1983, 35 m (USNM 131993, 1); sta. 7, Ponta do Maciel, Baia de Paranagua, 25°34′00″S, 48°25′00″W, col. Paulo Lana, 1 Jul 1986, 18 m (USNM 131994, 1); sta. 3, Ilhas Gereres, Baia de Paranagua, 25°29′00″S, 48°35′00″W, col. Paulo Lana, 2 Oct 1986, 10 m (USNM 131995, 1); sta. 2, Ponta da Cruz, Baia de Paranagua, 25°29′48″S, 48°29′30″W, col. Paulo Lana, 7 Nov 1981, 16 m (1, neotype USNM 131996).

Comments on material examined.—The material collected by Müller (1858) is no longer available (cf. Jones 1977:249). We obtained, thanks to Dr. Paulo da Cunha Lana, some specimens from the Brazilian coast which we consider close enough to the type locality to constitute authoritative material for the redescription of the species. The redescription is based on all four specimens; the designated neotype is indicated above.

Description.—All four specimens complete; varying in length from 15.4 to 62 mm. Thorax with 17 setigers; abdomen with 40 to 42 setigers. Nephridial papillae in groove medial to rudimentary parapodia of segment 2, close to branchial base; each papilla long and cylindrical. Dorsum with a large, transversely oriented hump on setiger 5 (Fig. 1g).

Fig. 1. *Terebellides klemani,* syntype 975: a, Anterior region, lateral view; b, Syntype 976b, neurosetae of right setiger 6; c, Syntype 976a, thoracic neurosetae of setiger 12, lateral view; d, Same from above; e–f, Same, abdominal uncini, frontal and lateral view. *Terebellides anguicomus,* neotype (USNM 131996): g, Anterior region, lateral view; h, Same, neurosetae of right setiger 5; i, Thoracic neurosetae, right setiger 8. *Terebellides carmenensis,* holotype (USNM 131989): j, Anterior region, lateral view; k, Same, neurosetae of left setiger 6, lateral view; l, Same, thoracic neurosetae, left setiger 15, lateral view; m, Same, from above.

Branchial lobes fused for most of their length. Inferior lobes much slenderer than superior ones. Both superior lobes tapering anteriorly; project forward; giving branchiae a 5-lobed appearance (Fig. 1g). Distal posterior region of each lamella with a row of slender papillar projections.

Parapodia of segments 2 and 3 (an asetigererous segment plus setiger 1) shifted dorsally in relation to other parapodia. Lateral lappets with well developed, ear-shaped projections from segment 2; projections are distinctly reduced by setiger 2; becoming increasingly smaller over next few parapodia.

Notopodial setae best developed in setiger 1; forming two or three very short rows of 10 to 20 long, finely limbate, pointed, slender capillaries. Four retractile spines present in neuropodium 5. Each spine bent at almost a right angle with a slender, curved tip (Fig. 1h). Long thoracic uncini in a single row of 6–8 in a torus; with a main fang, three secondary teeth and large numbers of tiny denticles (Fig. 1i). Abdominal tori with short multidentate uncini in single rows. Number of uncini varying between 19 and 49 per torus.

Anus terminal, surrounded by several blunt papillae.

Methylene blue staining pattern consisting of transverse stripes present on first 11 segments (ten setigers).

No tubes were present.

Discussion.—A characteristic feature of this species is the complete lack of notosetae in segment 2, making the number of thoracic setigers 17, rather than 18 as in all other species; the presence of lateral lappets with ear-shaped projections on segment 2 indicates that the first parapodia-bearing segment is asetigerous, corresponding to setiger 1 in the other species here considered.

Terebellides anguicomus has statistically distinctly fewer abdominal uncini per setiger than the other species here described. The numbers of both thoracic and abdominal uncini are significantly correlated with the size of the specimens.

A large dorsal hump is present in Müller's (1858) illustration of the species. This feature is present in this species and in *T. carmenensis,* new species; the relationship between these two species is further explored below.

Habitat.—*Terebellides anguicomus* has been reported from a variety of shallow water habitats along the Caribbean coast in sandy mud (Amaral 1980); how much of these reports refers to this species or to the other closely similar species described here is unknown. The organisms used in this study were found in silty and sandy sediments.

Distribution.—Brazilian coast, ?Caribbean Sea.

Terebellides carmenensis, new species
Fig. 1j–m

Terebellides cf. *klemani.*—Hernández-Alcantara, 1985.—Hernández-Alcantara & Solis-Weiss, 1991.

Material examined.—Sta. 4, San Julian (Boca de Puerto Real), Isla del Carmen, Campeche, Mexico. (Holotype USNM 131989.)

Description.—Holotype complete; with 18 thoracic and 37 abdominal setigers; 28.1 mm long and 2.8 mm wide; ovigerous with abdominal and part of thoracic body cavity filled with eggs.

Prostomium elongated; 2.6 mm in length. Nephridial papillae in groove between first notopodial bases and branchial stem (Fig. 1j). Large transverse hump on dorsum of setiger 7 (Fig. 1j).

Branchial lobes with long stalk; fused for most of their length. Two inferior lobes as wide as two superior ones. Branchial lamellae with distal row of slender papillar projections. Anterior extensions of superior lobes fused and tapering distally; giving branchiae a 5-lobed appearance.

Parapodia 3 and 4 shifted ventrally in relation to other parapodia. Rounded ear-shaped projections of lateral lappets best developed in setigers 1 and 2.

Notopodial setae of setiger 1 few in number and smaller than those of setiger 2. All notopodial setae slender, bilimbate, distally tapering, and narrow capillaries. Seven large retractile, double-curved acicular spines (Fig. 1k) present in neuropodium 6. Two paratypes with seven spines, two additional paratypes with six and five, respectively. Neuropodia 7 to 18 with single rows of about 12 long handled hooks. Each hook with main fang, two secondary teeth and many minute denticles distally (Fig. 1l, m). Each abdominal neuropodial torus with a row of 45 to 48 avicular multidentate uncini in holotype. In paratypes number of uncini in a torus varying from 39 to 54; apparently independent of size.

Segments crowded towards posterior end of the body. Pygidium a short cone. Anus terminal; surrounded by several blunt papillae.

No tube was found associated with this species.

Methylene blue staining pattern transverse stripes on first eleven setigers.

Discussion.—*Terebellides carmenensis* and *T. anguicomus* both have a conspicuous hump on the dorsum. In *T. carmenensis* the hump is on setiger 7 and in *T. anguicomus* it is on setiger 5. In addition, the latter lacks notopodial setae in segment 2; such setae are present in *T. carmenensis.*

The number of abdominal uncini per setiger is much larger in this species than in any other species examined in this study.

Habitat.—*Terebellides carmenensis* has been found in very shallow waters, associated with mangrove vegetation, in soft sediments (about ⅔ mud and ⅓ sand), at the entrance of Laguna de Terminos (Mexico).

Etymology.—The species is named for the area in which it was collected (Southeast of Isla del Carmen).

Terebellides parvus, new species
Figs. 2a–f, 3, Table 1

Material examined.—M-1 (USNM 131925, 5 paratypes); M-2 (USNM 131926, 42 paratypes); M-3 (USNM 131927, 16); M-5 (USNM 131928, 32 paratypes); M-6 (USNM 131929, 13 paratypes); M-7 (USNM 131930, 4 paratypes); M-8 (Australian Museum, 21 paratypes); M-9 (USNM 131931, 5); M-10 (USNM 131932, 2 paratypes); M-11 (USNM 131933, 10 paratypes); M-12 (BM(NH) 11 paratypes); M-13 (USNM 131934, 1); M-16 (Zoological Museum, Hamburg, 5 paratypes); M-20 (USNM 131935, 1 paratype); M-24 (USNM 131936, 2); M-25 (USNM 131937, 19); M-26 (USNM 131938, 11); M-27 (Allan Hancock Foundation, 8 paratypes); M-28 (USNM 131939, 9 paratypes); M-31 (USNM 131940, 2); M-34 (USNM 131941, 1); M-35 (USNM 131942, 3); M-36 (USNM 131943, 2); M-39 (USNM 131944, 4); M-40 (USNM 131945, 5 paratypes); M-41 (USNM 131946, 5); M-42 (USNM 131947, 17); M-45 (USNM 131948, 1 paratype); M-46 (USNM 131949, 1); M-47 (USNM 131950, 1); M-51 (USNM 131951, 2); M-52 (USNM 131952, 7); M-53 (USNM 131953, 36); M-54 (USNM 131954, 1); M-55 (USNM 131955, 1); M-58 (USNM 131956, 1); M-59 (USNM 131957, 3); M-60 (USNM 131958, 6); M-63 (USNM 131959, 1); M-65 (USNM 131960, 3); M-68 (USNM 131961, 2); M-69 (USNM 131962, 3); M-71 (USNM 131963, 2); M-75 (USNM 131964, 2); M-80 (USNM 131965, 30); M-81 (USNM 131966, 38 paratypes); M-84 (USNM 131967, 1); M-88 (USNM 131968, holotype and USNM 131969, 10 paratypes); M-90 (USNM 131970, 2); M-94 (USNM 131971, 3); M-95 (USNM 131972, 7); M-96 (USNM 131973, 58); M-100 (USNM 131974, 6); M-101 (USNM 131975, 5); M-107 (USNM 131976, 4); M-133 (USNM 131977, 6); M-139 (USNM 131978, 3); M-140 (USNM 131979, 14); M-141 (USNM 131980, 5); M-142 (USNM 131981, 5); M-143 (USNM 131982, 16 paratypes); M-144 (USNM 131983, 1); M-145 (USNM 131984, 12 paratypes); M-146 (USNM 131985, 3); M-147 (USNM 131986, 24 paratypes); M-148 (USNM 131987, 2); M-150 (USNM 131988, 2).

Description.—Holotype female with 18 thoracic and 25 abdominal setigers; 21.5 mm long and 2.5 mm wide; with prostomium and tentacles 27.5 mm long. Nephridial papillae located between base of first parapodium and base of branchial stalk.

Branchial lobes (Fig. 2a) with short stalks; stalks fused basally in holotype; lower half fused in some paratypes. All branchial lobes similar in size and shape in holotype; two inferior lobes considerably slenderer than superior ones in some paratypes. Superior branchial lobes anteriorly fused, prolonged and tapering, giving branchiae a 5-lobed appearance. Posterior edge of branchial lamellae with a distal row of small papillar projections.

First two parapodia shifted dorsally in relation to next following ones. Lateral lappets with distinct rounded ear-shaped projections in setigers 1, 2, and 3; projections are reduced over the next several setigers. Projections cover bases of notopodia in setiger 2 (Fig. 2a).

Notopodial setae of setiger 1 small and few in number; all notopodial setae slender, distally tapering, narrowly bilimbate capillaries. Five long retractile acicular spines present in setiger 6; each spine bent almost at a right angle, tapering to fine, slightly uptilted tips; small specimens have 3–4 spines (Fig. 2b). Setigers 7–18 have single rows of about 12 long-handled hooks. Each hook with a large main fang, two secondary teeth and a crest of many tiny denticles (Fig. 2c). Each abdominal neuropodial torus with a single row of usually 18–37 avicular multidentate uncini (Fig. 2d–f). Variability in number of hooks discussed below.

Posterior ends, including last 10 setigers held reflexed over dorsum when removed from tubes. Anus terminal, surrounded by several blunt papillae.

Tubes with a thin, flexible inner lining covered with plant debris and sand grains of varying sizes.

Methylene blue staining pattern transverse stripes in first eleven setigers.

Discussion.—The number of abdominal setigers present varies as illustrated in Fig. 3 and Table 1; specimens with fewer than 21 abdominal setigers are never mature. Below this number, there is a strong correlation between the size of the specimens and the number of abdominal setigers present; above this number, any correlation is rapidly lost.

The number of papillar projections on branchial lamellae appears to vary independent of the size and degree of maturity of the specimens. The number of acicular spines varies from 3 to 8 and is poorly related to the size of the specimens; small specimens have few acicular spines, but so do some of the large specimens.

The species is distinguished from closely related species by the low number of abdominal setigers and by the lack of a visible hump on the dorsum.

Habitat.—Found in root mats of *Rhizophora mangle* in very shallow water of normal salinity.

Etymology.—The name refers to the reduced number of abdominal setigers.

Terebellides lanai, new species
Fig. 2g–i

Material examined.—Sta. 6139, Operacao Sueste I, R/V *Almirante Saldanha,* 24°16′00′S, 46°01′02″W, col. Operacao Sueste I, R/V *Almirante Saldanha,* 21 Aug 1982, 45 m (holotype USNM 131990, 1 paratype USNM 131991); sta. 607B, Operacao Sueste I, R/V *Almirante Saldanha,* 26°51′00″S, 46°13′01″W, col. Operacao Sueste I, 2 Aug 1982, 50 m (2 paratypes, USNM 131992).

Description.—Holotype female with 18 thoracic and 38 abdominal setigers; 20 mm long and 1.5 mm wide.

The prostomium is large, with many long, slender tentacles (Fig. 2g). Nephridial papillae attached immediately medial to first notopodia; long, distally truncate cones; folded down in groove between first notopodia and base of branchial stalk.

Branchial lobes fused for most of their

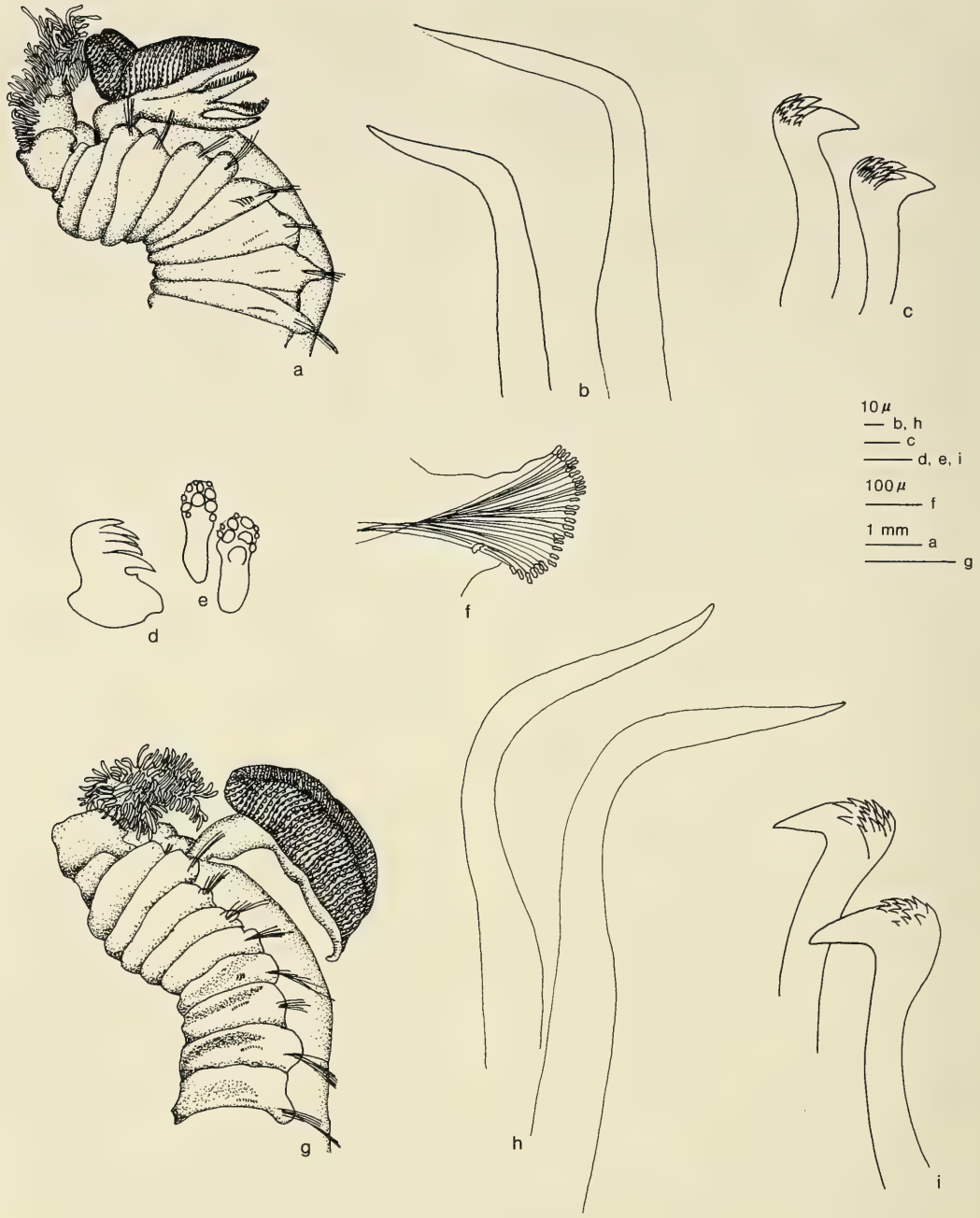


Fig. 2. *Terebellides parvus,* holotype (USNM 131968): a, Anterior region, lateral view; b, Same, neurosetae of left setiger 6; c, Same, thoracic neurosetae of left setiger 14; d, Same, abdominal uncinus of setiger 25, lateral view; e, Same, frontal view; f, Same, abdominal parapodium, setiger 25. *Terebellides lanai,* holotype (USNM 131990): g, Anterior reigon, lateral view; h, Same, neurosetae of left setiger 6; i, Same, thoracic neurosetae of left setiger 17.

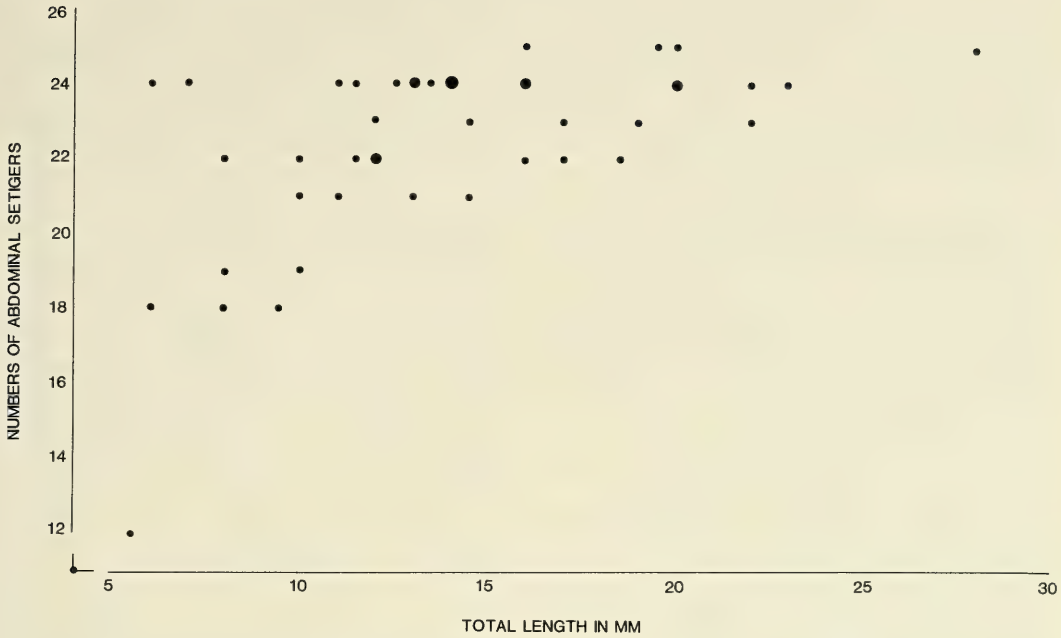


Fig. 3. Relation between total length and number of abdominal setigers in *Terebellides parvus*. The small dots represent single specimens, the larger dots two and three specimens, respectively.

length. Inferior lobes are slenderer than superior ones. Superior lobes tapering anteriorly; projecting forward; giving branchiae a 5-lobed appearance. Branchial lamellae with single row of small slender papillae near posterior edge.

Lateral lappets of first 5 setigers with rounded projections. Projections on setigers 1–2 largest; projections on setiger 3 slightly smaller than those on setigers 4–5 (Fig. 2g).

Notopodial setae of setiger 1 small and few in number; notosetae much larger and more numerous in second and following setigers. Notosetae slender, tapering, marginally narrowly limbate capillaries. Four large, distally pointed, retractile acicular spines in neuropodia of setiger 6 (Fig. 2h); each spine bent at nearly right angles and distally up-tilted. Neuropodia of setigers 7 to 18 with single rows of 8–10 long-shafted uncini. Most uncini with large main fangs and a crest of many denticles (Fig. 2i); in some uncini recognizable differentiation into 3 secondary teeth and crest of smaller teeth. Abdominal neuropodial tori with single row of 25 to 29 avicular multidentate uncini. Segments increasingly shorter and crowded towards pygidium; tori increasingly elongate posteriorly.

Table 1.—*Terebellides parvus*, new species. Summary statistics for relation between numbers of abdominal setigers and total length of specimen.

	Abdominal setigers	Total length
Maximum	25	28
Minimum	12	5.5
Mean	22.44	13.92
SD	2.48	5.00
Regression analysis		
Constant		−11.5086
SE of Y est		4.183815
R squared		0.31624
No. of observations		45
Degrees of freedom		43
X Coefficient(s)		*SE* of coef.
1.1332		0.2541

Anus terminal; fringed by several blunt papillae.

No tube currently associated with specimens.

Methylene blue staining without distinct pattern.

Discussion.—*Terebellides lanai* is distinguished from closely related species by having the branchiae fused for most of their length, a feature it shares with *T. anguicomus.* However, it lacks the dorsal hump present in the latter and has notopodial setae in 18 rather than in 17 thoracic segments as in *T. anguicomus.*

Habitat.—Tropical shallow waters, muddy and sandy sediments.

Distribution.—Known only from the type localities on the Brazilian coast.

Etymology.—Named for Dr. Paulo A. da Cunha Lana, eminent Brazilian polychaetologist. He provided the type material used in this study and has been a great help for all of us, especially the third author, on several occasions.

Overview of the Species Treated

The five species recognized in this study belong to the tropical group characterized by Williams (1984) as having forward branchial extensions and ear-shaped or rounded dorsal projections on one or more lateral lappets. Our material came from localities well within the ecological and geographical distribution pattern postulated for this group by Williams.

In addition the species resemble each other in that the first two parapodia are displaced dorsally in relation to those in the next following setigers.

Furthermore, we found a fringing row of papillar projections (=small tubercles) along the posterior region of the branchial lamellae in all five species. An examination of type material of other species of *Terebellides* deposited in the USNM showed that this feature is not present in all the species. Papillae are present in *T. reishi* Williams and in *T. californica* Williams; in the latter they are wider and flatter than in other species examined. Papillae are absent in *T. atlantis* Williams, *T. distincta* Williams, *T. eurystethus* Chamberlin, *T. japonica* Williams and *T. stroemi* Sars (observations on the latter not made on type material). The branchial papillae are difficult to observe unless the specimens are stained, and may for that reason have been overlooked by previous workers. The branchial papillae may turn out to be a useful additional character at the species level. The branchial papillae have so far been found only on species from shallow or shelf depths in relatively warm water; all species without papillae come from slope depths or from cold water.

All five species have low numbers of notosetae in setiger 1 (segment 2). We agree with Williams (1984) that the development of the notosetae in segment 2 is an important feature in the genus; thus the total absence of such setae in *T. anguicomus* must be considered an important character-state. Future analysis may show that the development of these setae form a transformation series, but at this time, it would be inappropriate to attempt an analysis of a small subset of the described species.

Other setae, including the neuropodial spines in setiger 6 (5 in *T. anguicomus*), are very similar in all five species.

Terebellides klemani and *T. anguicomus* may also be distinguished from each other by the presence of a distinctive dorsal hump in the latter; such a hump is also present in *T. carmenensis,* but on another setiger.

The staining pattern with methylene blue was of limited use: when present, it takes the form of transverse stripes across the first 11 segments. It was absent in *T. lanai* but very clearly seen in all specimens belonging to *T. anguicomus.* In *T. klemani,* it was clearly seen only in the smallest specimen, although in this case, its absence in the other specimens might be due to their deteriorated state. In *T. carmenensis* and *T. parvus,*

the staining pattern could be seen in most specimens.

Within each species the number of abdominal setigers varies very little with size in mature specimens (cf., Williams 1984, fig. 3). In small (immature) specimens the number of abdominal setigers varies with the size of the specimens. The character can be used safely in separating mature adults and also as a supportive feature for the identification of large immature specimens. In addition, the numbers of uncini in each abdominal torus appear to vary within narrow limits in each species. A more careful analysis may show that this character will also be useful for identifying at least adults.

Acknowledgments

This paper is Contribution number 301 from the Caribbean Coral Reef Ecology program under the direction of Dr. Klaus Rützler, supported in part by Exxon Corporation. Dr. Brian F. Kensley collected the Belize material together with Kristian Fauchald. Dr. Marian Pettibone gave us help with literature citations. We would like to thank Mr. Roy Oleröd for lending us type material. Dr. Paulo A. da Cunha Lana kindly donated the material from Brazil used in this study, for which we are grateful. The senior author would like to thank the Instituto de Ciencias del Mar y Limnologia and its ex-director, Dr. Ayala, The DGAPA (UNAM), and the Organization of American States for financial support, making her stay at the Smithsonian Institution possible. She would also like to thank Pablo Hernández-Alcantara, Ma. Nuria Mendez Ubach, and Andres Reda Deara for their participation in the field work in Mexico.

Literature Cited

Amaral, C. 1980. Anelidos Poliquetos do infralitoral em duas enseadas da regiao de Ubatuba. II. Aspectos ecologicos.—Boletim do Instituto Oceanografico Sao Paulo 29(1):69–87.

Banse, K. 1970. The small species of *Euchone* Malmgren (Sabellidae, Polychaeta).—Proceedings of the Biological Society of Washington 83:387–408.

Fauchald, K. 1977. The polychaete worms. Definitions and keys to the orders, families and genera.—Natural History Museum of Los Angeles County, Science Series 28:1–190.

Hartman, O. 1948. The marine annelids erected by Kinberg. With some notes on some other types in the Swedish State Museum.—Arkiv för Zoologi 42(1):1–137.

Hernández-Alcantara, P. 1985. Variación de la macrofauna béntica asociada al mangle rojo (*Rhizophora mangle*) en la Laguna de Terminos, Campeche, Mexico. Unpublished Prof. tesis, Universidad Nacional Autonoma de Mexico, Mexico D.F., 117 pp.

———, & V. Solis-Weiss. 1991. Ecological aspects of the polychaete populations associated to the red mangrove *Rhizophora mangle* at Laguna de Terminos, southeastern part of the Gulf of Mexico.—Proceedings of the Second International Polychaete Conference (in press).

Hessle, C. 1917. Zur Kenntnis der terebellomorphen Polychaeten.—Zoologiska Bidrag från Uppsala 5:39–258.

Jones, M. L. 1977. A redescription of *Magelona papillicornis* F. Müller. Pp. 247–266 *in* D. J. Reish & K. Fauchald, eds., Essays on polychaetous annelids in memory of Dr. Olga Hartman. Allan Hancock Foundation, University of Southern California, Los Angeles.

Kinberg, J. G. H. 1867. Annulata nova.—Öfversigt af Konglia Svenska Vetenskaps Akademiens Förhandlingar 23:337–357.

Müller, F. 1858. Einiges über die Anneliden Fauna der Insel St. Catharine an der Brazilianischen Küste.—Archiw für Naturgeschichte, Berlin 24(1):211–220.

Solis-Weiss, V., & K. Fauchald. 1989. Orbiniidae (Annelida: Polychaeta) from mangrove rootmats in Belize, with a revision of protoariciin genera.—Proceedings of the Biological Society of Washington 102:772–792.

Williams, S. 1984. The status of *Terebellides stroemi* (Polychaeta: Trichobranchidae) as a cosmopolitan species, based on a world-wide survey, including description of new species. Pp. 118–142 *in* P. A. Hutchings, ed., Proceedings of the First International Polychaete Conference, Sydney, published by the Linnean Society of New South Wales.

(VSW) Instituto de Ciencias del Mar y Limnologia, Universidad Nacional Autonoma de Mexico, Apdo Postal 70-305,

México, D.F. 04510, México; (KF) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (AB) Depto de Zoologia, Universidade Federal de Parana, CP 19 020 81504-Curitiba, Parana, Brasil.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 159–165

NICOMACHE OHTAI, NEW SPECIES (POLYCHAETA: MALDANIDAE) COLLECTED FROM THE HATSUSHIMA COLD-SEEP IN SAGAMI BAY

Tomoyuki Miura and Jun Hashimoto

Abstract.—A new maldanid polychaete species, *Nicomache ohtai,* is described from the Hatsushima cold-seep in Sagami Bay at a depth of 1163 m. The new species is very close to *N. venticola* from the hydrothermal vents of the northeastern Pacific, however it differs from the latter in having up to 19 rostrate uncini with 3–4 apical teeth in each neuropodium instead of up to 10 uncini with 2–3 teeth.

Studies on Japanese cold-seeps began as a French-Japanese cooperative project using the French deep-sea submersible *Nautile* in 1984 and were followed by multidisciplinary surveys using the Japanese submersible *Shinkai 2000* (Laubier et al. 1986, Miura 1988a). The collections from these programs have provided some interesting materials for polychaete taxonomy. To date, all of the polychaetes that have been described are directly associated with a larger host species at the seep sites (Miura 1988b; Miura & Laubier 1989, 1990). These associations include *Protomystides hatsushimaensis* attached to the openings of vestimentiferan tubes and species of the Nautiliniellidae living in the mantle cavities of bivalve mollusks. Free-living polychaetes have not been reported from these Japanese cold-seeps. However the second author did collect maldanid polychaetes within tubes that were attached to a dead shell of *Calyptogena soyoae* at 1163 m off Hatsushima.

Early important studies on the family Maldanidae were made by Arwidsson (1907, 1911a, 1911b). Imajima & Shiraki (1982) reviewed all Japanese maldanid polychaetes and reported 37 species including four species of the genus *Nicomache.* Intact specimens are required for the identification of maldanids because of the morphological importance of the posterior body region. In this study, a new species of the genus *Nicomache* is described based on intact specimens of some mature males and females.

The types are deposited in the National Science Museum, Tokyo (NSMT), the Japan Marine Science and Technology Center (JAMSTEC), and the National Museum of Natural History, Smithsonian Institution (USNM).

Genus *Nicomache* Malmgren, 1865

Nicomache ohtai, new species

Figs. 1–3

Material examined.—Western North Pacific, cold-seep communities off Hatsushima, Sagami Bay, Japan. DSRV *Shinkai 2000* Dive 450, 21 Oct 1989, 35°00.0′N, 139°13.5′E, 1163 m, collector J. Hashimoto, holotype (NSMT-Pol. H-326), 3 paratypes (USNM 127962), 4 paratypes (JAMSTEC); Dive 451, 22 Oct 1989, same site, collector K. Fujikura, 1 paratype (JAMSTEC); unmanned submersible *D3K,* Dive at Okinoyama Seep, Sagami Bay, 19 May 1989, 34°58.2′N, 139°31.4′E, 1116 m, 2 paratypes (JAMSTEC).

Description.—Complete paratypes 64–151 mm long, 1.7–2.8 mm wide, with 31–35 setigers (Table 1). Holotype 187 mm long, 3.5 mm wide including parapodia, with 32 setigers; with a single achaetous preanal

Table 1.—Measurement of type specimens of *Nicomache ohtai,* new species.

Specimen number	Number of setigers (achaetous rings)	Number of anal papillae	Body length (mm)	Body width (mm)	Sex
Dive 450					
1 (Holotype)	32 (+1)	22	187	3.5	female
2	32 (+1)	23	125	2.8	female
3	32 (+1)	18	120	2.4	?
4	32 (+1)	25	110	2.2	male
5	32 (+2)	24	151	2.6	male
6	35 (+0)	20	130	2.3	?
7	31 (+1)	18	139	2.5	?
8	33 (+0)	21	104	2.3	?
Dive 451					
1	31 (+1)	23	93	2.8	male
D3K					
1	32 (+1)	19	64	1.7	?
2*	25+	25	72	2.0	?
n	10	10	10	11**	
$\bar{x}$	32.2	21.3	122.3	2.46	
SD	1.1	2.5	33.5	0.47	

* With regenerated caudal end.
** Specimen *D3K* No. 2 included.

glandular ring well stained by Methyl Green. Color in alcohol pale, with slightly dark brown to reddish brown swollen areas on anterior and posterior segments.

Prostomium broadly rounded anteriorly; cephalic keel well defined, arched; nuchal slits situated on both sides of keel, curved, diverging anteriorly; mouth rounded, with thick lip (Fig. 1a, b).

Setigers 1–6 slightly longer than wide, flaring anteriorly, without collars (Fig. 1c); median segments very long, sometimes more than 4 times longer than wide; posterior setigers short, with well-defined glandular pads (Fig. 1d, e). Pygidium with dorsally shortened anal funnel bearing 22 papillae (Fig. 1d–f).

Parapodia biramous; first 3 neuropodia with 2–6 stout acicular spines (Fig. 2a, Table 2); following neuropodia with 9–12 rostrate uncini in anterior 2 and posterior 5 setigers, with 13–19 in middle 25 setigers (Fig. 3). Each uncinus with 3–4 teeth above main fang, numerous accessory spines on convex side and several subrostral fibrils (Fig. 2b). Notopodia with stout bilimbate capillaries (Fig. 2d) and short thin spinulose capillaries (Fig. 2c) on all setigers; with spirally spinulose capillaries (Fig. 2e) and a few short slender wavy capillaries (½ length of stout capillaries) on median and posterior notopodia (Fig. 2g).

Tube covered with coarse sand grains and mud.

Variation.—The total number of setigers varies from 31 to 35 ($\bar{X}$ = 32.2) in 10 complete specimens, with 6 having 32 (Table 1). In an exceptional paratype (Dive 450, No. 6) with 35 setigers, the last setigerous segment is merely recognized by the presence of its right parapodium. Thus the number is rather constant in the species.

Some early authors mentioned the number of preanal segments (glandular pads or rings) as an important character (e.g., Imajima & Shiraki 1982: the key to the species of the genus *Nicomache*), however the number is variable (0–2) in this new species. The

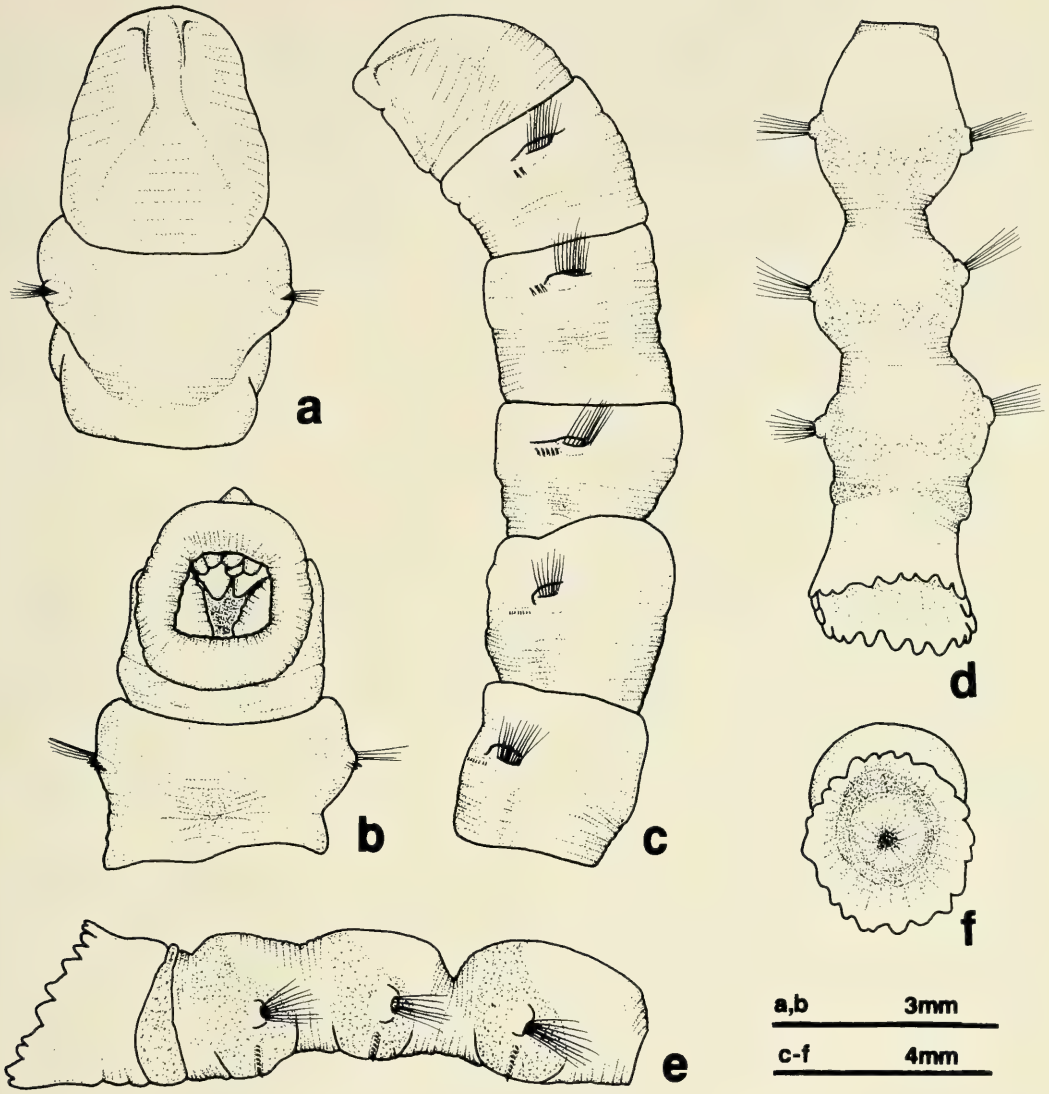


Fig. 1. *Nicomache ohtai* (Holotype): a, Anterior end, dorsal view; b, Same, ventral view; c, Anterior segments, lateral view; d, Posterior segments, dorsal view; e, Same, lateral view; f, Pygidium, posterior view.

number of papillae on anal funnel ranges from 18 to 25 ($\bar{X} = 21.3$, $n = 10$), with each papilla being very broad and sometimes subdivided.

The number of anterior acicular spines per parapodium ranges from 2 to 7 with the majority from 3 to 6 (Table 2). The number increases in the three succeeding setigers. For example, the average numbers of spines per parapodium in 11 specimens are 3.5, 4.1 and 5.2 on setigers 1, 2 and 3, respectively. The number of anterior setae seems to depend on the body size, however only the correlation of the number of rostrate uncini on parapodium 4L with the body width is significant ($R = 0.87$, $P \leq 0.001$).

Biology.—On some posterior segments, the spirally spinulose capillaries were cov-

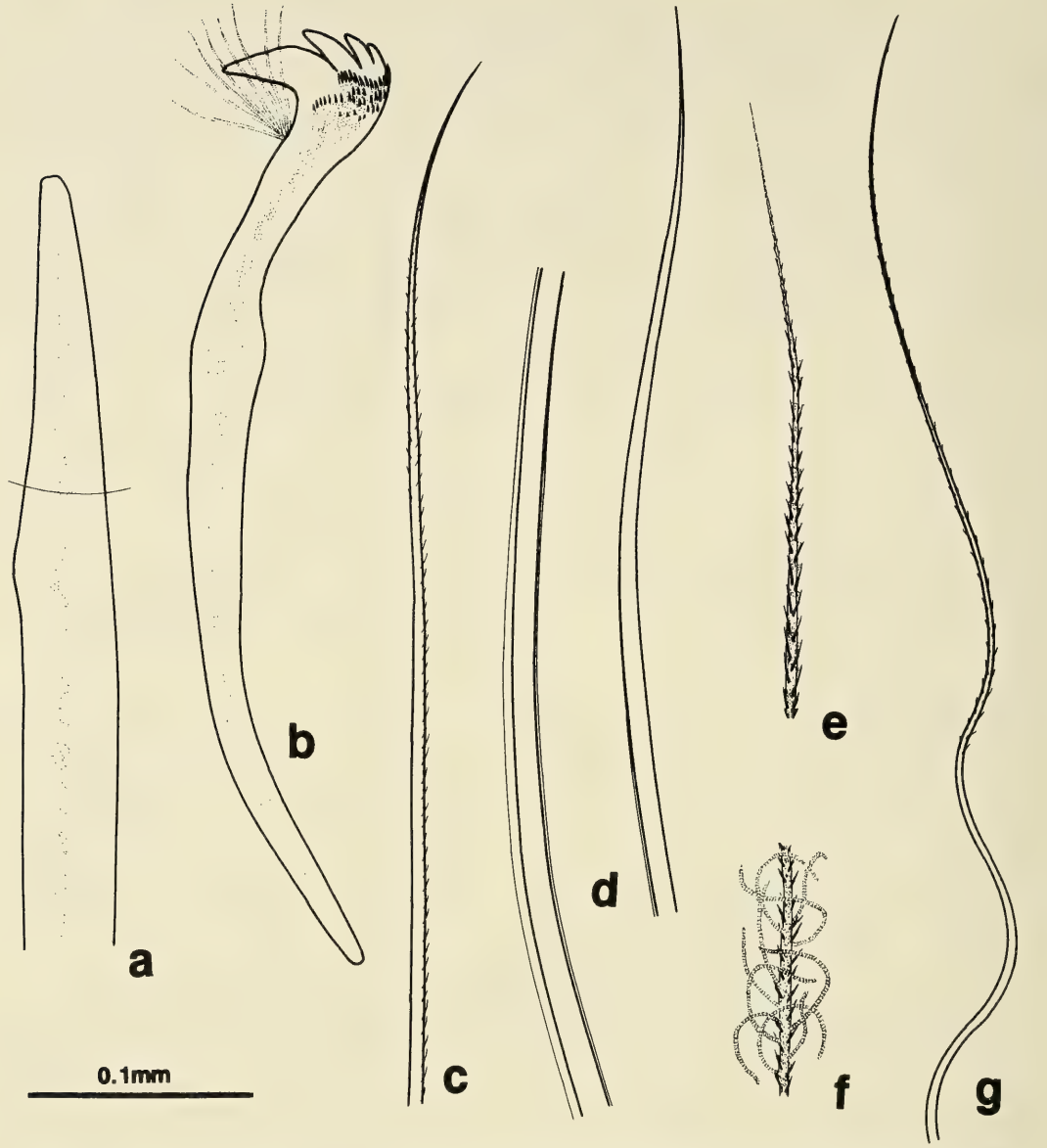


Fig. 2. *Nicomache ohtai* (Holotype): a, Acicular spine on setiger 1; b, Rostrate uncinus; c, Spinulose capillary; d, Bilimbate capillary; e, Distal end of spirally spinulose capillary; f, Part of same with *Beggiatoa*-like filaments; g, Short wavy capillary.

ered with numerous filaments (Fig. 2f), recalling the *Beggiatoa*-like bacteria found on some alvinellid polychaetes or on sediments of deep-sea hydrothermal vents (Desbruyères et al. 1985, Tunnicliffe et al. 1985).

Female specimens had oocytes in the coelom of mid-posterior segments. The oocytes are discoidal or hexagonal with the largest measuring about 150 μm × 50 μm.

Remarks.—In the genus *Nicomache,* 23 nominal species are recognized (Hartman 1959, Fauchald 1977, Blake 1985, Blake &

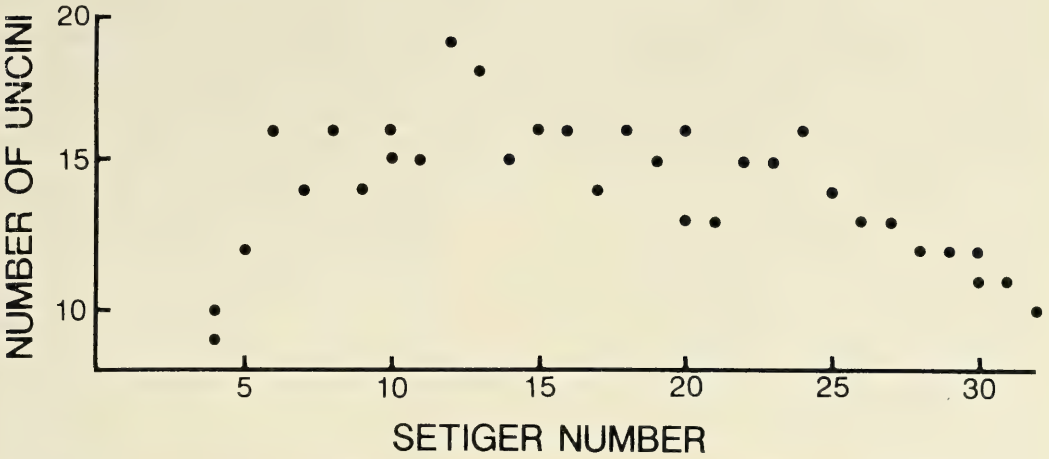


Fig. 3. Distribution of rostrate uncini in the holotype of *Nicomache ohtai,* new species.

Hilbig 1990). Most have 23 setigers or less and are easily distinguishable from *N. ohtai* which has more than 30 setigers. Two species have been described from deep-sea hydrothermal vents: *N. arwidssoni* Blake, 1985 and *N. venticola* Blake & Hilbig, 1990. *N. ohtai* is most similar to *N. venticola* in having 30 or more setigers, 22 anal papillae and up to 6 acicular spines in each of the first 3 setigers. *N. ohtai* differs from *N. venticola* in having up to 19 rostrate uncini with 3–4 apical teeth in each neuropodium instead of up to 10 uncini with 2–3 teeth and in the presence of the short wavy capillary instead of the absence. The absence of the long filamentous capillary in the two hydrothermal

Table 2.—Distribution of acicular spines and rostrate uncini (parenthesized numbers) on first four setigers in type specimens of *Nicomache ohtai,* new species.

Specimen number	Setiger number							
	1L	1R	2L	2R	3L	3R	4L	4R
Dive 450								
1	2	5	4	5	6	5	(10)	(9)
2	4	4	5	4	6	6	(9)	(7)
3	3	3	4	3	4	4	(7)	(6)
4	3	3	4	5	5	5	(7)	(7)
5	3	3	4	3	6	5	(8)	(8)
6	4	3	4	5	6	5	(8)	(6)
7	4	4	5	4	6	6	(8)	(10)
8	4	4	4	4	5	5	(7)	(7)
Dive 451								
1	4	4	6	4	6	7	(7)	(7)
D3K								
1	4	3	4	3	3	4	(6)	(6)
2	3	3	4	3	5	5	(6)	(6)
n	11	11	11	11	11	11	11	11
$\bar{x}$	3.5	3.5	4.4	3.9	5.3	5.2	7.5	7.2
SD	0.7	0.7	0.7	0.8	1.0	0.9	1.2	1.3

vent species was considered as an important character for separating them from other congeners (Blake 1985, Blake & Hilbig 1990). The presence of the short wavy capillary in *N. ohtai* is therefore thought to be an intermediate state between these two groups of species.

Nicomache mossambica Day, 1951 is another known species with more than 30 setigers. Both *N. mossambica* and *N. ohtai* have two or more acicular spines on the anterior three setigers, however the anal funnel of the former is cylindrical and differs from the dorsally shortened funnel of the latter.

Etymology.—The species is named in honor of Dr. S. Ohta of the Ocean Research Institute, University of Tokyo for his valuable advice on the sampling using submersibles.

Acknowledgments

The authors wish to thank the staff of the Japan Marine Science and Technology Center for their assistance in sampling on Dives 450 and 451 of *Shinkai 2000* and a dive of the unmanned submersible *D3K*. The manuscript benefited from the careful review by Dr. James A. Blake, Science Application International Corporation. Part of this study was supported by a grant-in-aid from Itoh Science Foundation.

Literature Cited

Arwidsson, I. 1907. Studien über die skandinavischen und arkischen Maldaniden nebst Zusammenstellung der übrigen bischer Arten dieser Familie.—Zoologische Jahrbücher, Supplement 9:1–308, 12, pls.

———. 1911a. On some Irish Maldanidae.—Proceedings of the Royal Irish Academy 29B:209–228, 3 pls.

———. 1911b. Die Maldaniden.—Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903 6(6):1–44, 2 pls.

Blake, J. A. 1985. Polychaeta from the vicinity of deep-sea geothermal vents in the eastern Pacific. I: Euphrosinidae, Phyllodocidae, Hesionidae, Nereididae, Glyceridae, Dorvilleidae. Orviniidae, and Maldanidae. Pp. 67–101 *in* Meredith L. Jones, ed., Hydrothermal vents of the eastern Pacific: an overview.—Bulletin of the Biological Society of Washington 6:1–566.

——— & B. Hilbig. 1990. Polychaeta from the vicinity of deep-sea hydrothermal vents in the eastern Pacific. II: New species and records from the Juan de Fuca and Explorer Ridge systems.—Pacific Science 44:219–253.

Day, J. H. 1951. The polychaete fauna of South Africa. Part 1: The intertidal and estuarine polychaeta of Natal and Mocambique.—Annals of the Natal Museum 12:1–67.

Desbruyères, D., F. Gaill, L. Laubier, & Y. Fouquet. 1985. Polychaetous annelids from hydrothermal vent ecosystems: an ecological overview. Pp. 103–116 *in* Meredith L. Jones, ed., Hydrothermal vents of the eastern Pacific: an overview.—Bulletin of the Biological Society of Washington 6:1–566.

Fauchald, K. 1977. The polychaete worms. Definitions and keys to the orders, families and genera.—Natural History Museum of Los Angeles County, Science Series 28:1–190.

Hartman, O. 1959. Catalogue of the polychaetous annelids of the world. Part 2.—Allan Hancock Foundation Publications, Occasional Paper 23: 355–628.

Imajima, M., & Y. Shiraki. 1982. Maldanidae (Annelida: Polychaeta) from Japan.—Bulletin of the National Science Museum, Tokyo 8A:7–88.

Laubier, L., S. Ohta, & M. Sibuet. 1986. Découverte de communautés animales profondes durant la campagne franco-japonaise KAIKO de plongées dans les fosses de subduction autour du Japon.—Comptes Rendus de l'Académie des Sciences, Paris, Série III 303:25–29.

Malmgren, A. J. 1865. Nordiska Hafs-Annulater.—Öfversigt af Kongl Vetenskaps-Akademiens Förhandlingar 21:51–110 & 181–192, 8 pls.

Miura, T. 1988a. Parasitic animals collected in a *Calyptogena*-dominant community developing off Hatsushima, Sagami Bay.—Japan Marine Science and Technology Center, Technical Reports 4:239–244 (in Japanese).

———. 1988b. A new species of the genus *Protomystides* (Annelida, Polychaeta) associated with a vestimentiferan worm from the Hatsushima cold-seep site.—Proceedings of the Japanese Society of Systematic Zoology 38:10–14.

——— & L. Laubier. 1989. *Nautilina calyptogenicola*, a new genus and species of parasitic polychaete on a vesicomyid bivalve from Japan Trench, representative of a new family Nautilinidae.—Zoological Science 6:387–390.

——— & ———. 1990. Nautiliniellid polychaetes

collected from the Hatsushima cold-seep site in Sagami Bay, with descriptions of new genera and species.—Zoological Science 7:319–325.

Tunnicliffe, V., S. K. Juniper, & M. E. de Burgh. 1985. The hydrothermal vent community on axial seamount, Juan de Fuca Ridge. Pp. 453–464 *in* Meredith L. Jones, ed., Hydrothermal vents of the eastern Pacific: an overview.—Bulletin of the Biological Society of Washington 6:1–566.

(TM) Faculty of Fisheries, Kagoshima University, 4-50-20 Shimoarata, Kagoshima 890; (JH) Japan Marine Science and Technology Center, 2-15 Natsushima-cho, Yokosuka 237, Japan.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 166–174

TWO NEW BRANCHIATE SCALE-WORMS (POLYNOIDAE: POLYCHAETA) FROM THE HYDROTHERMAL VENT OF THE OKINAWA TROUGH AND THE VOLCANIC SEAMOUNT OFF CHICHIJIMA ISLAND

Tomoyuki Miura and Jun Hashimoto

Abstract.—Two new polynoid polychaete species are described from the Kaikata Seamount, a volcanic front of Izu-Ogasawara Island-Arc system, and the Izena Hole, a hydrothermal vent in the Okinawa Trough. *Branchipolynoe pettiboneae,* found living commensally in the mantle cavities of deep-sea mussels, is close to *B. seepensis* in having large elytra and branchiae beginning on segment 3, however the new species differs from the latter in having the subbiramous parapodia with digitiform notopodia instead of the biramous parapodia with conical notopodia. *Opisthotrochopodus japonicus* differs from other congeners in having the ventral cirri and lacking the modified neuropodial organs on posterior parapodia.

Since the first branchiate scale-worm was found from the Galapagos Rift area (Pettibone 1984), 10 species attributed to 4 genera and 3 subfamilies have been described from various deep-sea hydrothermal vents and cold-seeps by Pettibone (1985a, 1985b, 1986, 1988, 1989a, 1989b) and another deep-sea species from experimentally enriched substrates by Desbruyères & Laubier (1988). Although several vents and seeps are known around Japan and many surveys using manned or unmanned deep-sea submersibles were carried out, none of the branchiate polynoids has been recorded. In this study, two new branchiate polynoid species are described from the Kaikata Seamount, a volcanic front of Izu-Ogasawara Island-Arc system, and the Izena Hole, a hydrothermal vent in the Okinawa Trough.

The types are deposited in the National Science Museum, Tokyo (NSMT), the Japan Marine Science and Technology Center (JAMSTEC), and the National Museum of Natural History, Smithsonian Institution (USNM).

Subfamily Branchipolynoinae Pettibone, 1984

Genus *Branchipolynoe* Pettibone, 1984

Branchipolynoe pettiboneae, new species

Figs. 1–3

Material.—Kaikata Seamount, off Chichijima Island, Western Pacific, DSRV *Shinkai 2000* Dive 339, 17 May 1988, 26°42.3′N, 141°05.0′E, 580 m, collector J. Naka, associated with deep-sea mussel, holotype (NSMT Pol.-H 327). Izena Hole, Okinawa Trough, Dive 364, 10 Sep 1988, 27°16.0′N, 127°05.0′E, 1340 m, collector M. Kimura, associated with deep-sea mussels, paratype (USNM 131183), 3 paratypes (JAMSTEC).

Description.—Holotype 27 mm long, 11 mm wide including parapodia (4 mm without parapodia), with 21 segments, including first achaetous tentacular segments. Body short, slightly tapered anteriorly and posteriorly, flattened ventrally and arched dorsally (Fig. 1a, b). Pairs of long ventral papillae on segments 11 and 12; pygidium with pair of anal cirri, not fused basally (Fig. 1b).

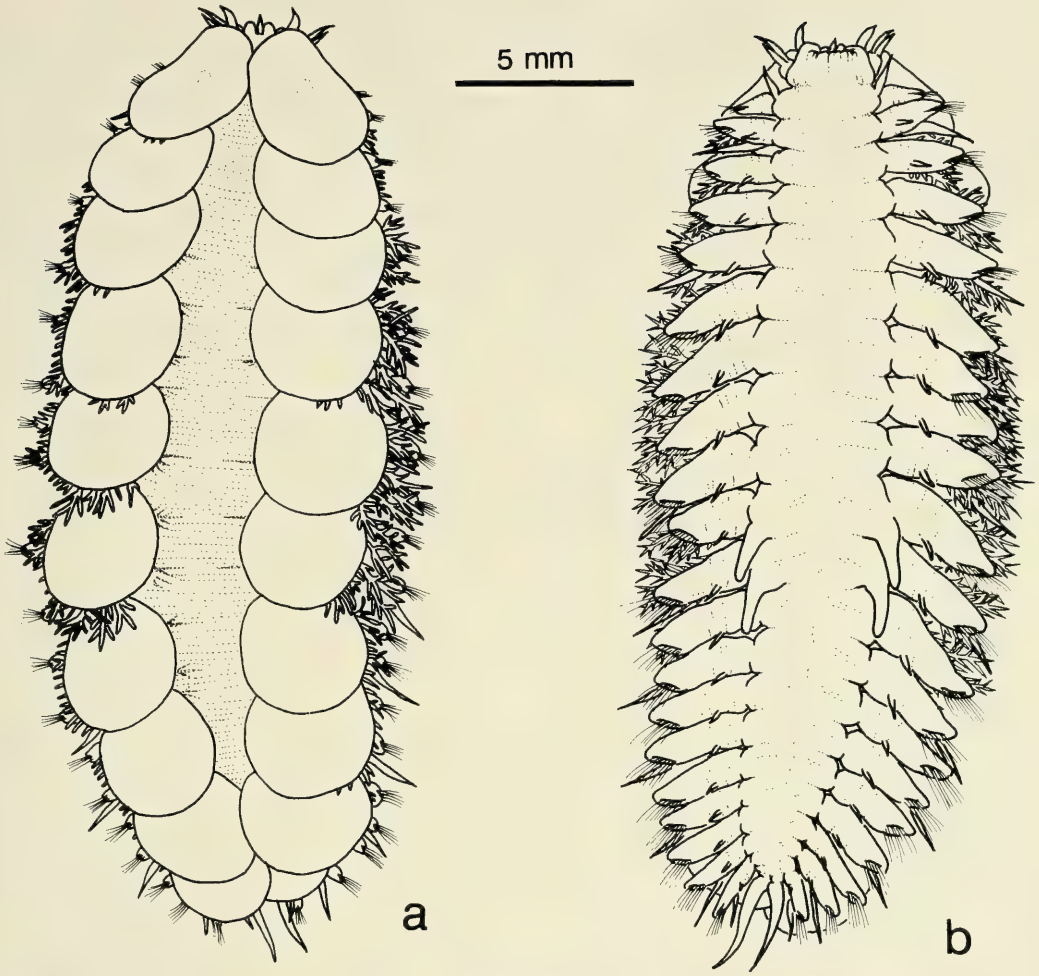


Fig. 1. *Branchipolynoe pettiboneae,* Holotype: a, Dorsal view; b, Ventral view.

Elytra 10 pairs, moderately large, oval, opaque, smooth, present on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, and 19. First pair and last 2 pairs of elytra covering dorsum completely, others leaving middle third of body uncovered (Fig. 1a). Dorsal cirri on non-elytragerous segments with short cylindrical cirrophores, short styles with slender tips, extending to tips of neurosetae; dorsal tubercles indistinct. Branchiae starting on segment 3, arborescent, separated into upper larger and lower smaller groups (Fig. 2a, e–h).

Prostomium oval, bilobed, with rounded anterior lobes, lacking frontal filaments (Fig. 2a). Median antenna, short, conical, with slender tip, without distinct ceratophore. Ventrolateral palps thick, smooth, tapered, extending beyond prostomium, with slender tips. First tentacular segment achaetous, fused to prostomium, not distinct dorsally; tentaculophores lateral to prostomium with 2 pairs of tentacular cirri, slightly shorter than palps (Fig. 2a, b).

Segment 2 with first pair of elytrophores, with subbiramous parapodia; notopodium very small, digitiform, with 4 notosetae, scarcely projecting beyond notopodium;

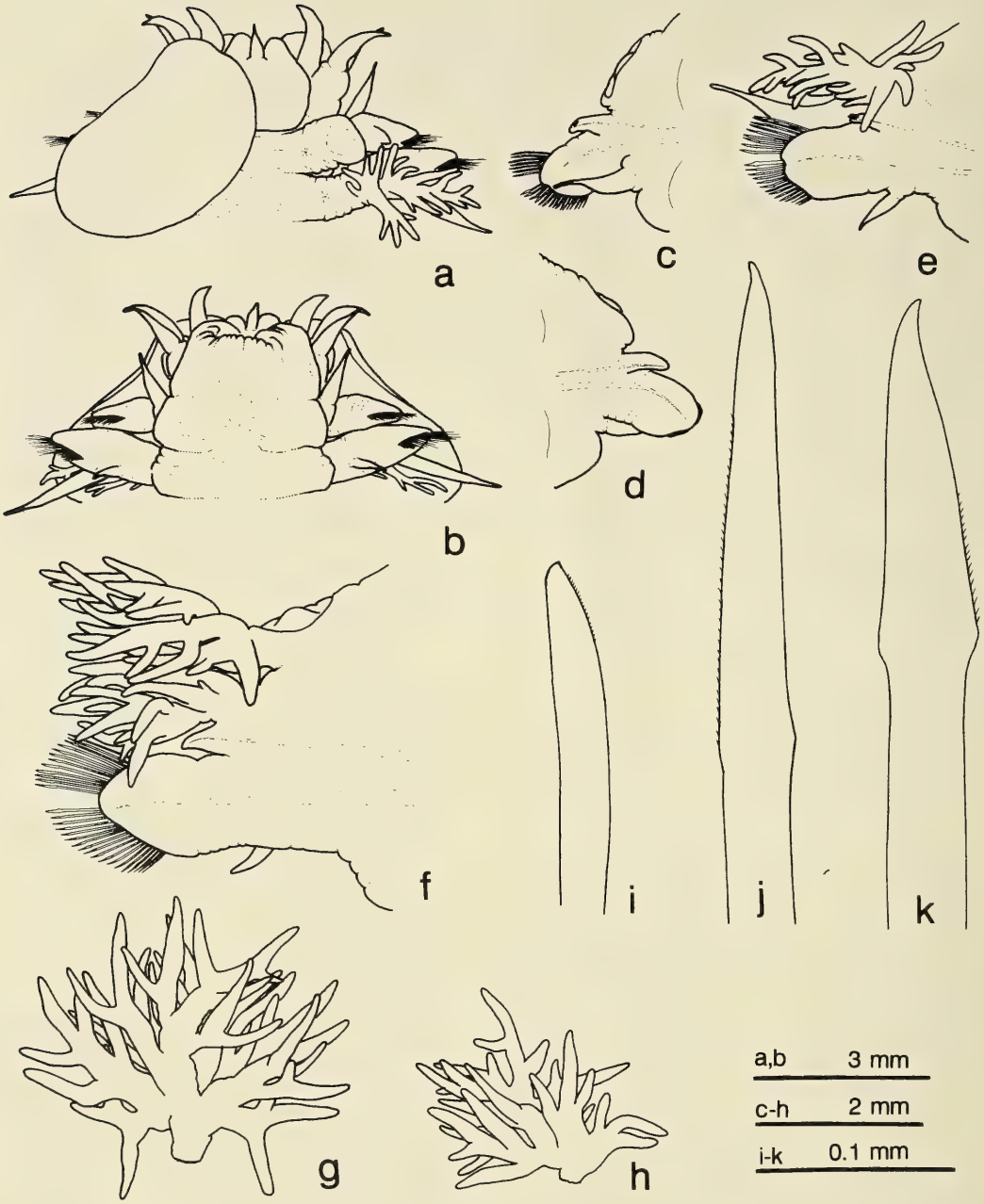


Fig. 2. *Branchipolynoe pettiboneae,* Holotype: a, Anterior end, dorsal view; b, Same, ventral view; c, Right elytragerous parapodium from segment 2, elytron removed, anterior view; d, Same, posterior view; e, Right cirrigerous parapodium from segment 3, anterior view; f, Right elytragerous parapodium from segment, 9, elytron removed, anterior view; g, Upper group of branchiae from segment 9, lateral view; h, Lower group of same, lateral view; i, Notoseta from segment 15; j, Supraacicular neuroseta from same; k, Upper subacicular neuroseta from same.

neuropodium large with slightly bilobed presetal acicular lobe and rounded postsetal lobe (Fig. 2c, d). Segment 3 with dorsal cirri, arborescent branchiae, and parapodia similar to segment 2 (Fig. 2a, b, e). Following parapodia subbiramous, with short, small, digitiform notopodia and long rounded neuropodia (Fig. 2f). Notosetae few, up to 5 per parapodium, scarcely projecting, stout, slightly tapered, with serrated distal margin (Fig. 2i). Neurosetae stouter than notosetae, tapered, wider subdistally, with serrated distal margin and slightly hooked tips (Fig. 2j, k). Distal serrated parts of supraacicular neurosetae (Fig. 2j) longer than subacicular neurosetae (Fig. 2k). Upper subacicular neurosetae (Fig. 2k) stouter than supraacicular and lower subacicular neurosetae.

Variation in paratypes (Fig. 3a–g).—From the Izena Hole of the Okinawa Trough, about 1300 km West of the type locality, the Kaikata Seamount, four polynoids associated with deep-sea mussels were collected. The host bivalve from the Izena Hole is presumably an undescribed species of the genus *Bathymodiolus,* while that of the holotype from the Kaikata Seamount is a species of the genus *Adula.* A careful study of these polynoids, however, leads us to consider that the polynoids from both hydrothermal areas belong to the same species. In three paratypes, the muscular pharynx was extended (Fig. 3a, b). There are 5 pairs of dorsal and ventral papillae around the opening and 2 pairs of smooth jaws inside. The smallest paratype measures 16 mm long by 5.7 mm wide including parapodia with 21 segments (Fig. 3a, b). All morphological characters agree with those of the holotype, except for the anterior region. In this small paratype, the first pair of elytra did not cover the anterior dorsum completely (Fig. 3a), perhaps caused by the extended pharynx and its consequent inflation of the anterior segments. In the smallest paratype, the upper subacicular neuroseta (Fig. 3f) is much stouter than the lower neurosetae (Fig. 3g). Supraacicular and lower subacicular neurosetae are subequal in width (Fig. 3e, g). The neurosetae (Fig. 3e–g) are stouter than the notosetae (Fig. 3d). These differences in the width of the setae are more obvious in the smallest paratype than in the holotype and other paratypes.

Etymology.—The species is named in honor of Dr. Marian H. Pettibone of the National Museum of Natural History, Smithsonian Institution, in our deep respect for her excellent papers on the family Polynoidae.

Remarks.—In the genus *Branchipolynoe,* two previously known species are clearly distinguishable from each other by morphological characters. *B. symmytilida* Pettibone, 1984, from the Galapagos Rift, has small elytra and branchiae starting on segment 2, while *B. seepensis* Pettibone, 1986, from the Gulf of Mexico, has large elytra and branchiae beginning on segment 3. *B. pettiboneae* is very close to *B. seepensis* in these characters. They differ in the structure of the notopodia. The new species has the subbiramous parapodia, with reduced digitiform notopodia and up to 5 notosetae, while *B. seepensis* has the biramous parapodia, with large conical notopodia and moderate number of notosetae (up to 20 in adults).

Subfamily Branchinotogluminae Pettibone, 1985

Genus *Opisthotrochopodus* Pettibone, 1985

Opisthotrochopodus japonicus, new species

Figs. 4–6

Material.—Kaikata Seamount, off Chichijima Island, *Shinkai 2000* Dive 404, 29 Apr 1989, 26°42.3′N, 141°05.0′E, 625 m, collector J. Hashimoto, sieving from bottom sediments, holotype (NSMT Pol.-H 328); paratype (USNM 131184).

Description.—Holotype 3.7 mm long, 3.1 mm wide including parapodia, with 21 seg-

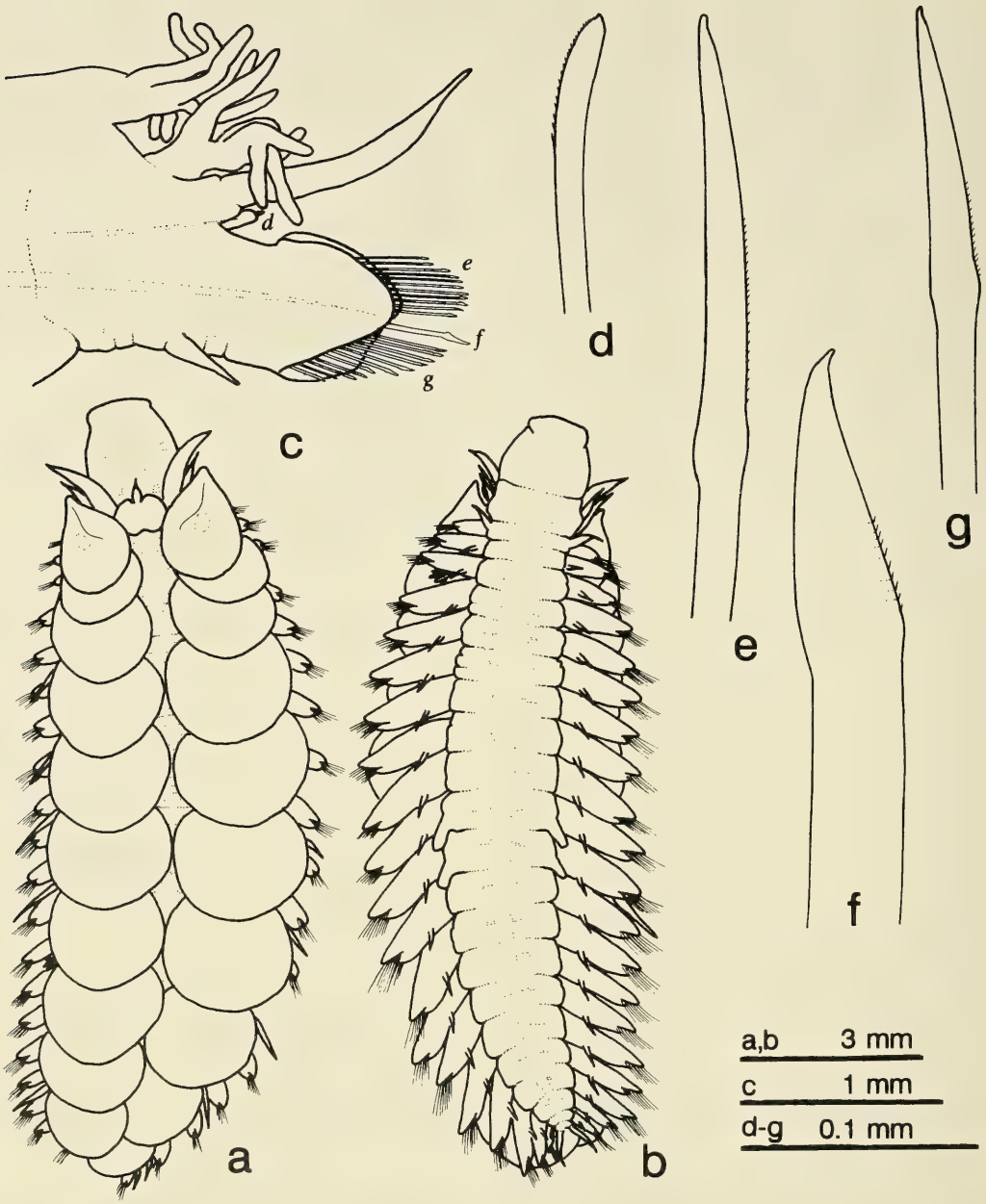


Fig. 3. *Branchipolynoe pettiboneae,* paratype (USNM 131183): a, Dorsal view, pharynx extended; b, Ventral view; c, Right cirrigerous parapodium from segment 10, posterior view; d, Notoseta from same; e, Supraacicular neuroseta from same; f, Upper subacicular neuroseta from same; g, Lower subacicular neuroseta from same.

ments. Body short, flattened, tapering slightly anteriorly and posteriorly, with parapodia longer than trunk width (Fig. 4a, b). Pharynx not extended, with two pairs of dark jaws. Pair of long segmental ventral papillae present on segment 12; 5 pairs of squarish ventral lamellae present on following segments 13 to 17 (Fig. 4b). Pygidium with 2 short anal cirri (Fig. 4a, b, e, f).

Elytra 10 pairs, covering dorsum com-

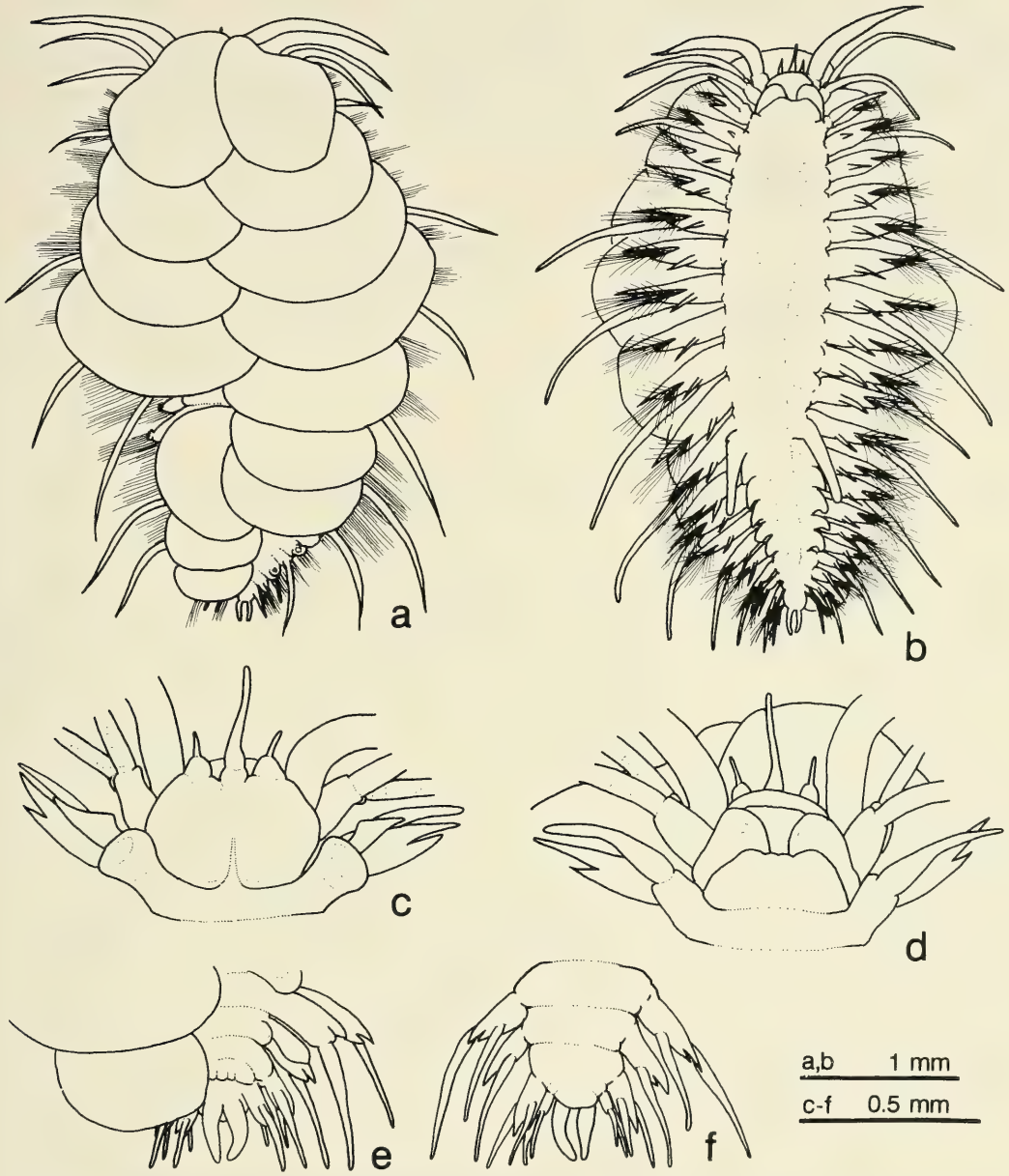


Fig. 4. *Opisthotrochopodus japonicus,* Holotype: a, Dorsal view; b, Ventral view; c, Anterior end, dorsal view, setae not shown; d, Same, ventral view; e, Posterior end, dorsal view, setae not shown; f, Same, ventral view.

pletely, present on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19. Elytra very large, overlapping, oval, delicate, without tubercles or papillae (Fig. 4a, e). Dorsal cirri on non-elytragerous segments 3, 6, 8, 10, 12, 14, 16, 18, 20, 21, with cylindrical cirrophores on dorso-posterior side of notopodia and very long smooth styles; dorsal tubercles nodular (Fig. 5b, d). Branchiae arborescent, in two groups on segments 3–14, not conspicuous on segment 15, and in form of single globular papilla on segment 16.

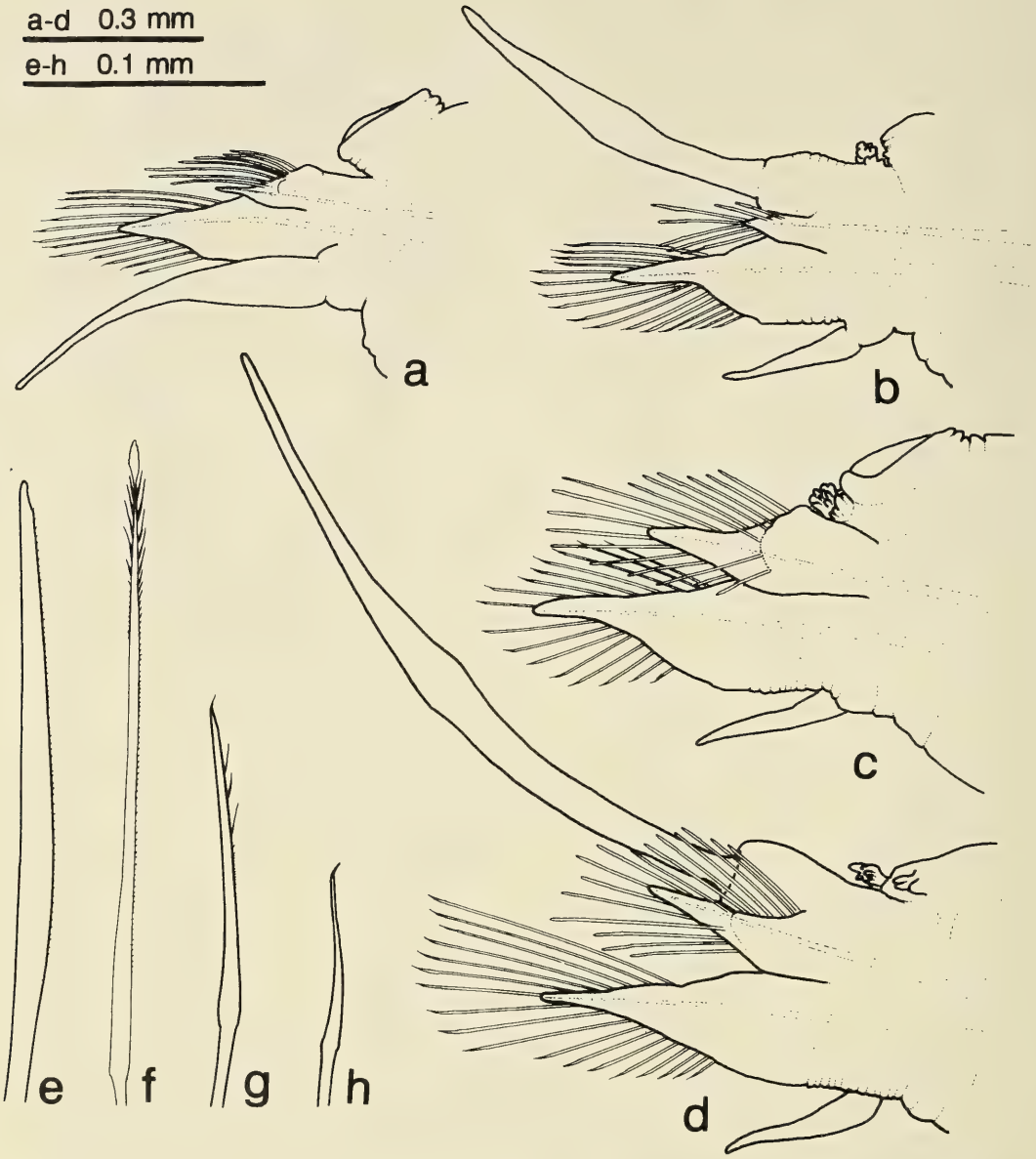


Fig. 5. *Opisthotrochopodus japonicus,* Holotype: a, Right elytragerous parapodium from segment 2, anterior view; b, Right cirrigerous parapodium from segment 3, anterior view; c, Right elytragerous parapodium from segment 9, anterior view; d, Right cirrigerous parapodium from segment 10, anterior view; e, Notoseta from same; f, Supraacicular neuroseta from same; g, Upper subacicular neuroseta from same; h, Lower subacicular neuroseta from same.

Bilobed prostomium with short cylindrical anterior lobes terminating in cirriform tips and non-ocular paired oval areas well-stained by Methyl Green, but without eyes; median antenna with bulbous ceratophore in anterior notch and short slender style; palps long, tapered, smooth, about 5 times as long as prostomium (Fig. 4a–d).

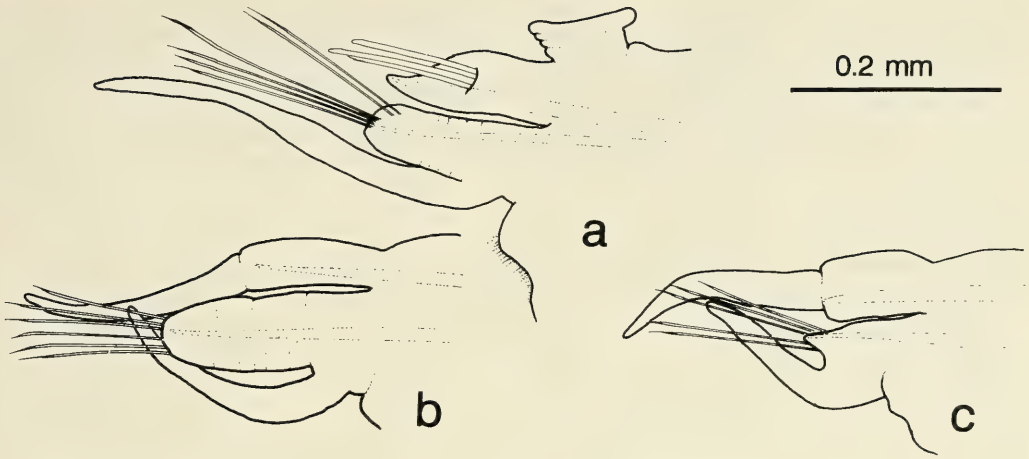


Fig. 6. *Opisthotrochopodus japonicus,* Holotype: a, Right elytragerous parapodium from segment 19, anterior view; b, Right cirrigerous parapodium from segment 20, anterior view; c, Same from segment 21, anterior view.

Tentacular segment not distinct dorsally; tentaculophores lateral to prostomium, achaetous, with 2 pairs of long tentacular cirri as long as palps; dorsal tentacular cirri slightly longer than ventral (Fig. 4b–d). Segment 2 with first pair of elytrophores, biramous parapodia, and long slender ventral buccal cirri; notopodium with distinct acicular lobe and stout notosetae, without notopodial bract; neuropodium with long acicular lobe and slender neurosetae (Fig. 5a).

Parapodia biramous, except for those on segments 20 and 21 (Fig. 5a–d). Notopodia conical, with prominent acicular processes, without distinct notopodial bracts except on segment 19. Neuropodia larger and longer than notopodia, with conical presetal acicular lobes and short rounded postsetal lobes. Ventral cirri short, tapered.

Notosetae numerous, stouter than neurosetae, tapered to blunt tips, with faint spinous margin (Fig. 5e). Neurosetae very numerous, slender. Supraacicular neurosetae with 2 rows of subdistal prominent spines and inflated tips (Fig. 5f). Upper subacicular neurosetae faintly spinous, with short capillary tips and a few long subdistal spines on spinous margin (Fig. 5g). Lower subacicular neurosetae smooth, with short capillary tips (Fig. 5h).

Posterior 3 segments compressed with parapodia much smaller and directed posteriorly (Fig. 4b, e, f). Parapodia of elytragerous segment 19 biramous, with rami similar in length; notopodium with thickened dorsal bract and few stout notosetae; neuropodium with faint spinous long neurosetae; ventral cirrus tapered, cirriform, longer than neurosetae (Fig. 6a). Parapodium of segment 20 subbiramous, with notopodial acicular lobe fused to cirrophore of dorsal cirrus, without notosetae; neuropodium cylindrical, similar to that of segment 19; ventral cirrus tapered, cirriform, shorter than neurosetae (Fig. 6b). Parapodium of segment 21 subbiramous, with notopodium fused to dorsal cirrus; neuropodium small, with short conical acicular lobe; ventral cirrus tapered, similar to that of segment 20 (Fig. 6c).

Etymology.—The specific name, *japonicus,* is based on the collecting site, the Kaikata Seamount in Japan.

Remarks.—The genus *Opisthotrochopodus* differs from other branchiate polynoids in having a pair of long segmental papillae on segment 12, 5 or 6 pairs of short lamellae on the following segments, and the compressed posterior segments. The genus consists of 4 species from various hydrothermal

vents: *O. alvinus* Pettibone, 1985, from the Galapagos Rift, East Central Pacific, *O. tunnicliffeae* Pettibone, 1988, from the Northeast Pacific Explorer and Juan de Fuca Ridges, *O. marianus* Pettibone, 1989, from the Mariana Back-Arc Basin, West Central Pacific, and *O. japonicus,* from the Kaikata Seamount, Northwest Pacific. *O. alvinus* is easily distinguishable from other congeners in having the greatly modified parapodia with wheel organ on segment 20. *O. tunnicliffeae* has the ventral cirri on posterior parapodia as in the new species, however it is separated from the latter in the presence of the balloon organ and the harpoon neurosetae on segment 20. In the genus *O. japonicus* is most close to *O. marianus* in the setal composition and the structure of parapodia, however it differs from the latter in the absence of the neuropodial oval lamellae on segment 21 instead of the presence.

Acknowledgments

The authors wish to thank the staff of the Japan Marine Science and Technology Center for their assistance in sampling at dives 339, 364 and 404 of *Shinkai 2000.* The manuscript benefited from the careful review by Dr. Marian H. Pettibone, Smithsonian Institution. Part of this study was supported by a grant-in-aid from Itoh Science Foundation.

Literature Cited

Desbruyères, D., & L. Laubier. 1988. Exploitation d'une source de matière organique concentrée dans l'océan profond: intervention d'une annélide polychète nouvelle.—Comptes Rendus de l'Académie des Sciences, Paris, Série III 307: 329–335.

Pettibone, M. H. 1984. A new scale-worm commensal with deep-sea mussels on the Galapagos hydrothermal vent (Polychaeta: Polynoidae).—Proceedings of the Biological Society of Washington 97:226–239.

———. 1985a. An additional new scale worm (Polychaeta: Polynoidae) from the hydrothermal rift area off western Mexico at 21°N.—Proceedings of the Biological Society of Washington 98:150–157.

———. 1985b. Additional branchiate scale-worms (Polychaeta: Polynoidae) from Galapagos hydrothermal vent and rift-area off western Mexico at 21°N.—Proceedings of the Biological Society of Washington 98:447–469.

———. 1986. A new scale-worm commensal with deep-sea mussels in the seep-sites at the Florida Escarpment in the eastern Gulf of Mexico (Polychaeta: Polynoidae: Branchipolynoinae).—Proceedings of the Biological Society of Washington 99:444–451.

———. 1988. New species and new records of scaled polychaetes (Polychaeta: Polynoidae) from hydrothermal vents of the Northeast Pacific Explorer and Juan de Fuca Ridges.—Proceedings of the Biological Society of Washington 101: 192–208.

———. 1989a. New species of scale-worms (Polychaeta: Polynoidae) from the hydrothermal rift-area of the Mariana back-arc basin in the western central Pacific.—Proceedings of the Biological Society of Washington 102:137–153.

———. 1989b. Polynoidae and Sigalionidae (Polychaeta) from the Guaymas basin, with descriptions of two new species, and additional records from hydrothermal vents of the Galapagos rift, 21°N, and seep-sites in the Gulf of Mexico (Florida and Louisiana).—Proceedings of the Biological Society of Washington 102:154–168.

(TM) Faculty of Fisheries, Kagoshima University, 4-50-20 Shimoarata, Kagoshima 890, Japan; (JH) Japan Marine Science and Technology Center, 2-15 Natsushimacho, Yokosuka 287, Japan.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 175–180

A NEW SPECIES OF *HESIOCAECA* (POLYCHAETA: HESIONIDAE) FROM HYDROTHERMAL VENTS AT THE MARIANA BACK-ARC BASIN WITH NOTES ON OTHER POLYCHAETES

James A. Blake

Abstract.—*Hesiocaeca hessleri* (family Hesionidae) is newly described from hydrothermal vents at the Mariana back-arc basin and is only the second species to be described in this deep-sea genus. The new species is most closely related to North Atlantic congeners rather than species from the eastern Pacific. Descriptive comments are provided on two additional polychaetes, *Nicomache arwidssoni* (family Maldanidae) and *Amphisamytha galapagensis* (family Ampharetidae), that have also been found at this site.

As part of continuing exploration of active hydrothermal vents, an expedition to the Mariana back-arc basin in the central Pacific was conducted in April and May 1987. Back-arc basins develop behind volcanic arcs bordering the deep trenches that occur where one plate dips beneath another. The Mariana back-arc basin is one such site that has developed in proximity to the Marianas Trench and the volcanic archipelago that composes the Marianas Islands. Back-arc spreading centers are isolated from mid-oceanic ridges and provide an opportunity to study faunas that are isolated from other hydrothermal vent ecosystems.

Polychaetes from the Mariana back-arc basin have been reported by Pettibone (1989) and Desbruyères & Laubier (1989). Pettibone (1989) described four new species of Polynoidae that belonged to four genera and three subfamilies that had been previously described by her from hydrothermal vents in the eastern Pacific. Likewise, Desbruyères & Laubier (1989) described a new species of *Paralvinella,* a genus known from all of the previously studied vent areas in the eastern Pacific. These results indicate that the isolation of the Mariana back-arc basin has been sufficient for polychaetes to evolve at the species level, but not at the generic level. Additional polychaetes collected by Dr. Robert Hessler were given to me for examination. These included representatives of the families Hesionidae, Ampharetidae, and Maldanidae. The material included a new species of the genus *Hesiocaeca,* previously known from the western North Atlantic, the ampharetid *Amphisamytha galapagensis,* known from all previously studied vent ecosystems, and the maldanid *Nicomache arwidssoni,* previously known from the Galapagos Rift hydrothermal vent area. Records and descriptive data are presented for each of these species along with remarks on their occurrence and systematic relationships.

The collections are deposited in the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C. 20560.

Family Hesionidae
Hesiocaeca hessleri, new species
Fig. 1

Material examined.—Western central Pacific in Mariana back-arc basin, *Alvin* Dive 1843, Alice Springs, 4 May 1987, 18°12.6′N, 144°42.4′E, 3640 m, holotype and 6 paratypes (USNM 132660-1).

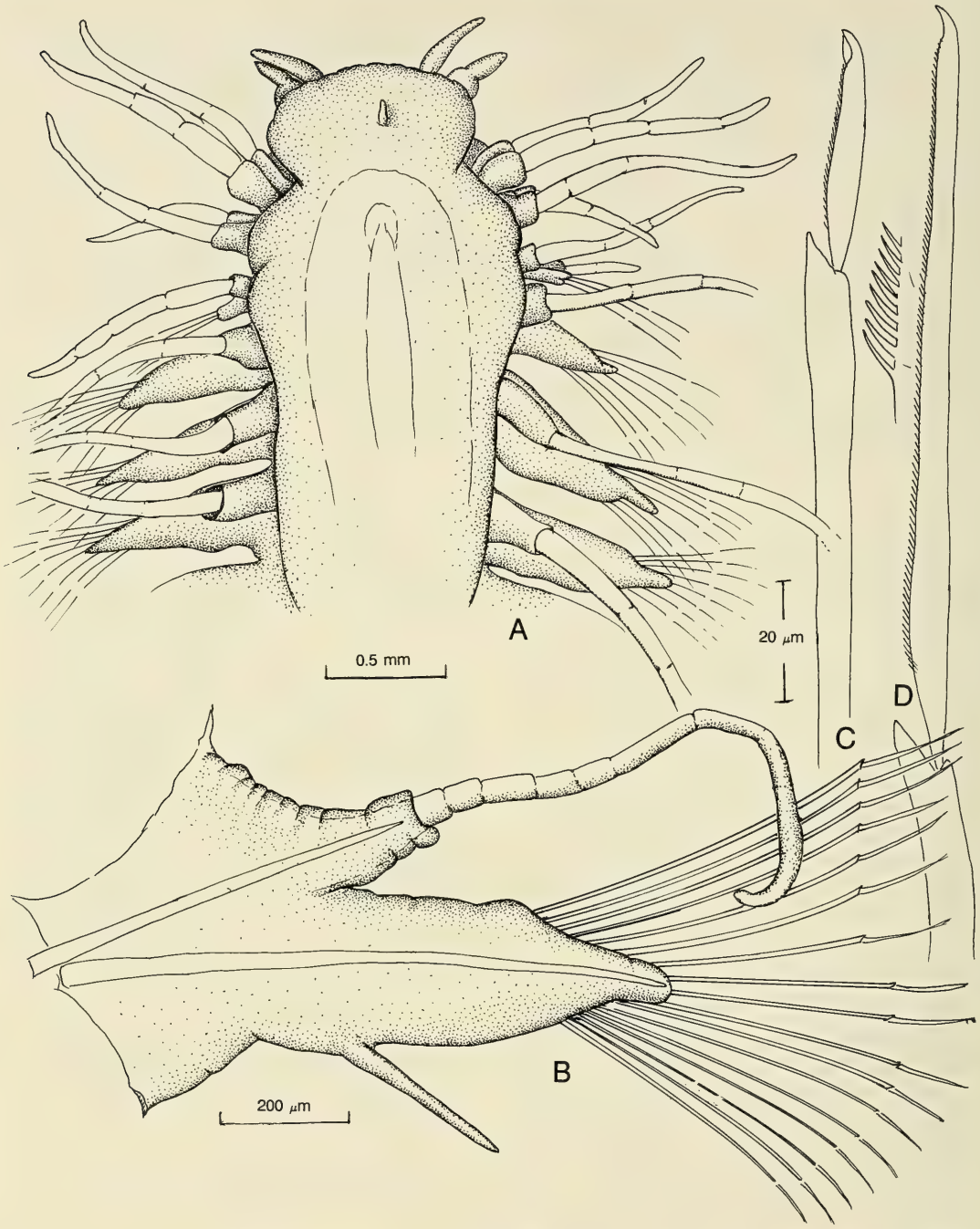


Fig. 1. *Hesiocaeca hessleri* (USNM 132601). A, Anterior end and 4 setigers in dorsal view. B, Middle parapodium, posterior view. C, Compound falciger with short blade. D, Compound falciger with long blade (inset not to scale).

Description.—Small species, widest anteriorly, tapering posteriorly; holotype measuring 5.0 mm long and 1.2 mm wide including parapodia for 27 setigers; largest paratype measuring 4.8 mm long and 1.0 mm wide for 28 setigers. Color in alcohol: flesh.

Prostomium wider than long, broad anteriorly, slightly tapering posteriorly before merging with body; 2 smooth, tapering, frontal antennae on anterior margin; with short medial antenna in middle of prostomium; palps biarticulated with enlarged bases and tapering tips; eyes absent (Fig. 1A). Proboscis not observed. Tentacular cirri numbering four pairs, inserted on 2 achaetous segments (Fig. 1A); tentacular cirri and dorsal cirri with weak, indistinct articulations.

Parapodia subbiramous with reduced notopodia bearing long, weakly articulated dorsal cirri and internal aciculum (Fig. 1B). Neuropodium well developed, with elongate presetal lobe with rounded apex, with imbedded aciculum and spreading fascicle of compound falcigers; each falciger with shaft bearing prominent tooth; blades short to long, each with fine denticles on one edge and unidentate tip bearing thin hoodlike membrane (Fig. 1C, D); falcigers with longest blades in dorsal and middle part of fascicle, setae with shortest blades ventralmost; ventral cirrus thin, fingerlike, nonarticulated. Pygidium simple, lacking cirri.

Remarks.—*Hesiocaeca hessleri* is only the second species of this deep-sea genus to be discovered and is most closely related to *H. bermudensis* Hartman, the type species, originally described from the Gay Head–Bermuda Transect off Bermuda in 1000–2500 m (Hartman 1965, Hartman & Fauchald 1971). *Hesiocaeca hessleri* differs from *H. bermudensis* in having a short medial antenna in the middle of the prostomium, instead of a long one at the posterior margin, and in having a prostomium that is twice as wide as long, instead of one that is nearly as wide as long.

Family Maldanidae

Nicomache arwidssoni Blake, 1985

Nicomache arwidssoni Blake, 1985:97–100, fig. 20.

Material examined.—Western central Pacific in Mariana back-arc basin, *Alvin* Dive 1843, Alice Springs, 4 May 1987, 18°12.6′N, 144°42.4′E, 3640 m, 4 specimens (USNM 132662).

Remarks.—The specimens are all small. The largest and only complete specimen is 7 mm long and 0.5 mm wide for 21 setigerous segments. The specimens are clearly juveniles and are referred to *Nicomache arwidssoni* on the basis of the number of setigers and the presence of 4 apical teeth on the rostrate hooks. This species was originally described from hydrothermal vent areas on the Galapagos Rift and the East Pacific Rise at 21°N (Blake 1985). A closely related species, *N. venticola,* has been discovered at hydrothermal vent sites on the Explorer and Juan de Fuca Ridge (Blake and Hilbig 1990). This latter species differs from *A. arwidssoni* in having 27–32 setigerous segments, instead of 21–22, and by having 2–3 apical teeth on the rostrate hooks, instead of 4. The present specimens are referred to *A. arwidssoni,* despite the separation in the geographic range.

Family Ampharetidae

Amphisamytha Hessle, 1917

Amphisamytha galapagensis Zottoli, 1983

Amphisamytha galpagensis Zottoli, 1983: 379–391, figs. 1–3.—Desbruyères et al., 1985:103–116.—Grassle, 1985:714; 1986:327.—Grassle et al., 1985:443–452.—Tunnicliffe et al., 1986:407.—Tunnicliffe, 1988:352.—Blake & Hilbig, 1990:244–246.

Material examined.—Western central Pacific in Mariana back-arc basin, *Alvin* Dive 1830, 15 April 1987, Burke Field, Anemone Heaven, Snow Pit, 18°10.9′N,

144°43.2′E, 3660 m, 6 specimens (USNM 132663); *Alvin* Dive 1836, 27 April 1987, Burke Field, Snail Pit, 3660 m, 18°10.9′N, 144°43.2′E, 1 adult and 9 juveniles (USNM 132664); *Alvin* Dive 1843, Alice Springs, 4 May 1987, 3640 m, 18°12.6′N, 144°42.4′E, 6 specimens (USNM 132665).

Description.—Body widest anteriorly, tapering posteriorly to narrow pygidium lacking appendages. Prostomium broad, smooth, lacking glandular ridges, forming dorsal lip of mouth; eyes lacking. Segments 1–3 fused, achaetous, located immediately posterior to prostomium; in juveniles, capillary notosetae transitional on segment 3. Numerous smooth oral tentacles emerging from mouth opening. Four pairs of smooth branchiae arising from achaetous segments on either side of dorsal mid-line of body. Segment 4 equals first setiger of adult; 17 thoracic setigers, uncini beginning on setiger 4; abdominal uncinigerous segments numbering 15–18. Notopodia reduced to simple lobes bearing fascicle of 6–7 limbate capillary notosetae; neuropodia including prominent pinnules bearing 15–20 uncini in single row; each uncinus with rounded basal prow surmounted by 4 teeth; small fine denticles observed on third, or largest, tooth.

Remarks.—I have compared these specimens carefully with the original account presented by Zottoli (1983) from the Galapagos Rift vents, as well as specimens from the Juan de Fuca Ridge and Gorda Ridge and can find no significant morphological differences. The species has now been reported from the seep site on the Florida Escarpment, the eastern Pacific vent sites at 13°N, Galapagos Rift, 21°N, Guaymas Basin, Gorda Ridge, and Juan de Fuca Ridge (Grassle 1986; Blake & Hilbig 1990; Blake, unpublished data), and now the Mariana back-arc basin in the central Pacific. The only apparent differences between the Mariana specimens and the original description from the Galapagos Rift were the number of abdominal uncinigerous segments (15–18, instead of 12–15) and the presence of fine denticles on some of the larger apical teeth of the uncini. These differences appear to merely represent small scale genetic variation in widespread populations and are insufficient to warrant a separate species designation. Specimens examined from the Gorda Ridge and Juan de Fuca Ridge have 12–14 abdominal uncinigerous segments. It is likely that the small denticles are actually present in the other populations and have simply been overlooked. The fact that *A. galapagensis* maintains its morphological constancy over such wide geographic distances is remarkable and suggests that evolutionary change is slow in this well adapted species. The high densities recorded for this species in the Guaymas Basin (2267 individuals per m^2) in soft sediments by Petrecca & Grassle (1989) strongly support the concept that *A. galapagensis* is an opportunistic species in hydrothermal vent ecosystems.

Discussion

The total number of polychaete species now recorded from the Mariana back-arc basin is 8: Polynoidae (4), Hesionidae (1), Maldanidae (1), Ampharetidae (1), and Alvinellidae (1). Six of these species are only known from the site, while two are also known from the eastern Pacific vent locations. All belong to genera that were previously known from deep-sea habitats or other vent localities.

The two known species of *Hesiocaeca, H. hessleri* and *H. bermudensis,* are known from the central Pacific and western North Atlantic, respectively. The first is associated with hydrothermal vents, while the second is a component of ambient infaunal communities in soft sediments. A closely related undescribed species, lacking a medial antenna, has been discovered at the cold-seep site on the Florida Escarpment. Thus, a group of closely related deep-sea hesionid

polychaetes having four pairs of tentacular cirri occurs in the Atlantic and central Pacific, but not in the eastern Pacific. This relationship is similar to the discovery of taxonomic similarity between shrimps of the genus *Rimicaris* on the mid-Atlantic Ridge and the Mariana back-arc basin (Hessler et al. 1988) and suggests a possible pattern of dispersal and adaptive radiation between Atlantic and Pacific faunas via Indian Ocean pathways. At present, however, no samples have been taken from Indian Ocean hydrothermal vents to prove or disprove this hypothesis.

The community composition of the Mariana back-arc basin differs structurally from communities at vent locations in the eastern Pacific and includes faunal elements having relationships to both the Atlantic and eastern Pacific. Polychaetes, however, have evolved only new taxa at the species level.

Acknowledgments

I am grateful to Robert Hessler for providing the specimens on which this paper is based. The *Alvin* dives on which these collections were taken were divided into two legs in 1987. Harmon Craig was Chief Scientist for the first, and Robert Hessler was Chief Scientist for the second. An early draft of the manuscript benefitted from comments by Brigitte Hilbig.

Literature Cited

Blake, J. A. 1985. Polychaeta from the vicinity of deep-sea geothermal vents in the eastern Pacific I: Euphrosinidae, Phyllodocidae, Hesionidae, Nereididae, Glyceridae, Dorvilleidae, Orbiniidae, and Maldanidae. Pp. 67–101 *in* M. L. Jones, ed., Hydrothermal vents of the eastern Pacific: an overview.—Bulletin of the Biological Society of Washington 6:1–566.

———, & B. Hilbig. 1990. Polychaeta from the vicinity of deep-sea hydrothermal vents in the eastern Pacific II: new species and records from the Juan de Fuca and Explorer Ridge systems.—Pacific Science 44:219–253.

Desbruyères, D., F. Gaill, L. Laubier, & Y. Fouquet. 1985. Polychaetous annelids from hydrothermal vent ecosystems: an ecological overview. Pp. 103–110 *in* M. L. Jones, ed., Hydrothermal vents of the eastern Pacific: an overview.—Bulletin of the Biological Society of Washington 6: 1–566.

———, & L. Laubier. 1989. *Paralvinella hessleri,* new species of Alvinellidae (Polychaeta) from the Mariana back-arc basin hydrothermal vents.—Proceedings of the Biological Society of Washington 102:761–767.

Grassle, J. F. 1985. Hydrothermal vent animals: distribution and biology.—Science 229(4715):713–717.

———. 1986. The ecology of deep-sea hydrothermal vent communities.—Advances in Marine Biology 23:301–362.

———, L. S. Brown-Leger, L. Morse-Porteous, R. Petrecca, & I. Williams. 1985. Deep-sea fauna of sediments in the vicinity of hydrothermal vents. Pp. 443–452 *in* M. L. Jones, ed., Hydrothermal vents of the eastern Pacific: an overview.—Bulletin of the Biological Society of Washington 6:1–566.

Hartman, O. 1965. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas.—Allan Hancock Foundation Publications Occasional Paper No. 28: 1–378.

———, & K. Fauchald. 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas Part II.—Allan Hancock Monographs in Marine Biology No. 6:1–327.

Hessler, R., P. Lonsdale, & J. Hawkins. 1988. Patterns on the ocean floor.—New Scientist 117(1605):47–51.

Petrecca, R., & J. F. Grassle. 1989. Notes on fauna from several deep-sea hydrothermal vent and cold seep soft-sediment communities. Pp. 279–283 *in* G. R. McMurray, ed., Gorda Ridge—a seafloor spreading center in the United States exclusive economic zone. Springer-Verlag, New York, 300 pp.

Pettibone, M. H. 1989. New species of scale-worms (Polychaeta: Polynoidae) from the hydrothermal rift-area of the Mariana back-arc basin in the western central Pacific.—Proceedings of the Biological Society of Washington 102:137–153.

Tunnicliffe, V. 1988. Biogeography and evolution of hydrothermal-vent fauna in the eastern Pacific Ocean.—Proceedings of the Royal Society of London B233:347–366.

———, A. M. Botros, M. E. de Burgh, A. Dinet, H. P. Johnson, S. K. Juniper, & R. E. McDuff. 1986.

Hydrothermal vents of Explorer Ridge, northeast Pacific.—Deep-Sea Research 33:401–412.

Zottoli, R. 1983. *Amphisamytha galapagensis,* a new species of ampharetid polychaete from the vicinity of abyssal hydrothermal vents in the Galapagos Rift, and the role of this species in rift ecosystems.—Proceedings of the Biological Society of Washington 96:379–391.

Science Applications International Corporation, 89 Water Street, Woods Hole, Massachusetts 02543.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 181–183

A NEW *ADMETULA* (GASTROPODA; CANCELLARIIDAE) FROM SOUTH AFRICA

Richard E. Petit and M. G. Harasewych

Abstract.—*Admetula epula* is described on the basis of seven specimens taken from the gut contents of fish caught between Cape St. Blaize and Port Elizabeth, Republic of South Africa. This new species can be distinguished from all Recent congeners on the basis of its lack of varices and its smooth outer lip.

The cancellariid genus *Admetula* Cossmann, 1889 was erected to contain five Eocene species from the Paris Basin, and is well represented in Paleogene and Neogene Tethyan faunas. The genus survives in the Recent fauna along continental margins at depths ranging from 75–700 m. Recent species referable to this genus include: *Admetula garrardi* Petit, 1974, from the western rim of the Pacific, *A. atopodonta* (Petit & Harasewych, 1986) from the central Philippines, *A. deroyae* Petit, 1970, from the Galapagos Islands, *A. bayeri* (Petit, 1976) and *A. vossi* (Petit, 1976), both from the western Atlantic, and *A. cornidei* (Altimira, 1978) from off northwestern Africa. Seven specimens, all taken from the gut contents of fish caught off southernmost Africa, represent an additional species of *Admetula* that is described herein.

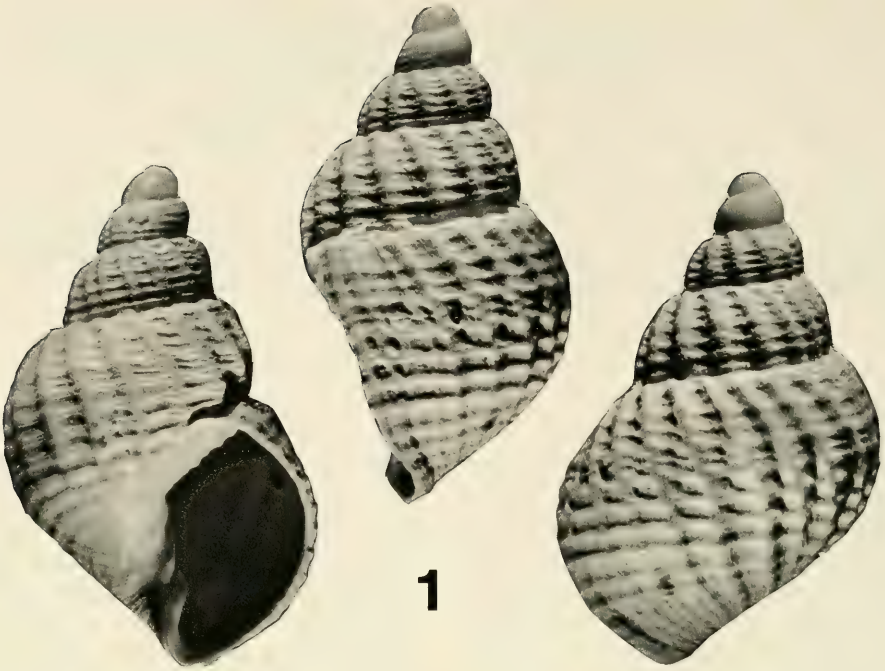
Abbreviations used in the text: NM, Natal Museum, Pietermaritzburg; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

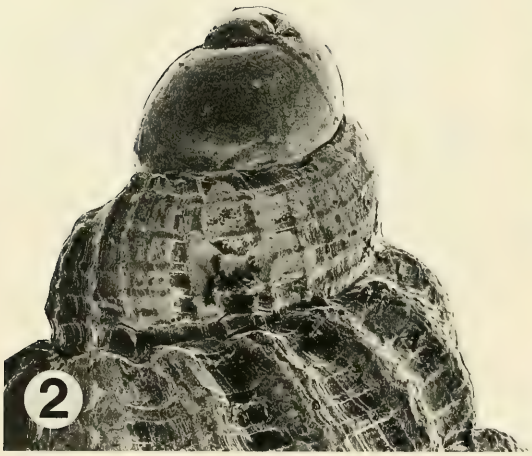
Ademetula epula, new species
Figs. 1–3, Table 1

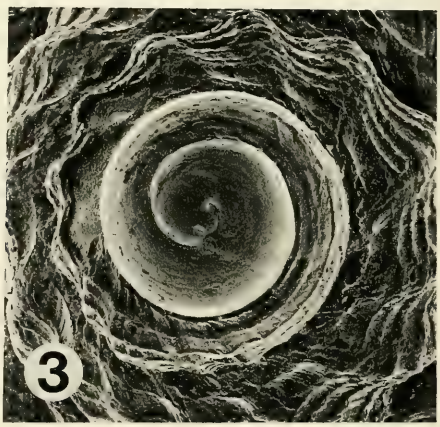
Diagnosis.—A small species with ovately conical shell lacking varices. Outer lip of aperture smooth, neither crenulate nor with lirae.

Description.—Shell (Fig. 1, Table 1) small, reaching 10.2 mm, heavy, ovately conical, with rounded anterior. Protoconch (Figs. 2, 3) of 1¾ smooth, erect whorls, aligned with coiling axis of teleoconch. Transition to teleoconch marked by appearance of 4–5 low, broad, spiral cords, followed ½ whorl later by 3–4 closely spaced axial bands, equal to spiral cords in prominence. Thereafter, axial sculpture consists of regularly spaced, rounded, strongly prosocline ribs (11–12 on first teleoconch whorl, 16–20 on body whorl). Teleoconch with up to 4 strongly convex whorls. Suture impressed behind small, rounded shoulder. Spiral sculpture of 11–15 major cords on body whorl, with single, weaker cord between adjacent major cords. Aperture ovate, deflected from coiling axis by 12–14°. Outer lip thin, smooth within. Inner lip adpressed posteriorly, with an angle of 122–130° formed between the parietal region and the columella. Parietal region with 5 or 6 equally-spaced, raised ridges overlying anteriormost spiral cords of previous whorl. Columella with two sharp columellar folds and siphonal fold, all equally prominent. Anterior slope of shell steep, with no clear distinction between body whorl and siphonal canal. Shell color white. Periostracum light greenish-yellow, consisting of thin, closely-spaced lamellae, with fine hairs at intersections of spiral cords and axial ribs.

Material examined.—Holotype (NM B7266/T2817); Paratypes 1, 2 (NM B873); Paratype 3 (USNM 845610); Paratype 4 (Petit collection); between Cape St. Blaize and Port Elizabeth, Republic of South Af-







Figs. 1–3. 1, *Admetula epula,* apertural, lateral and dorsal views of the holotype, 8.0×. Apical (Fig. 2) and lateral (Fig. 3) views of the protoconch, both 50×.

rica, ex pisce. Paratype 5 (NM A4817), off Cape St. Blaize area, ex gut *Congiopodus spinifer,* Jun 1976. Paratype 6 (NM B1050), off Cape St. Blaize, ex pisce, Jun 1975.

Type locality.—Between Cape St. Blaize and Port Elizabeth, Republic of South Africa.

Etymology.—The Latin *epula,* meaning banquet or feast, is considered appropriate as all known specimens have been collected from the gut contents of bottom feeding fish.

Remarks.—On the basis of its size and shell morphology, *Admetula epula* appears to be most closely related to *A. cornidei.* It

Table 1.—*Admetula epula,* new species. Measurements of shell characters. Linear measurements in mm (n = 5).

Character	Mean	σ	Range
Shell length (SL)	9.47	0.49	8.86–10.23
Aperture length (AL)	5.42	0.41	4.92–6.12
AL/SL	0.572	0.02	0.544–0.598
No. of whorls, protoconch	1.71	0.08	1.55–1.75
No. of whorls, teleoconch	3.47	0.12	3.25–3.60
Spire angle	55.2°	0.81°	54.0°–56.5°
Axial ribs on body whorl	19.0	1.55	16–20

can be distinguished from *A. cornidei* by its more elevated spire, by its smooth outer lip that lacks apertural lirae, and by its rounded rather than tabulate shoulder. The western Pacific Recent species *Admetula garardi* and *A. atopodonta,* as well as *A. evulsa* (Solander, 1766), the Eocene type species of the genus, all differ in attaining nearly twice the size of the African species, as well as in having distinct varices at increments of 90–120°, protoconchs deviated from the coiling axis of the shell, and lirae within the outer lip.

The fact that both specimens of *A. cornidei* and all seven specimens of *A. epula* are 9–11 mm in length suggests that this represents the adult size of these species. Nothing is known of the biology of *Admetula epula* other than that *Congiopodus spinifer* (Smith), one of the fish from which this species was taken, normally inhabits depths of 55–146 m (Smith & Heemstra 1986).

Acknowledgments

We thank Dr. R. N. Kilburn, Natal Museum, Pietermaritzburg, Republic of South Africa, for bringing this new species to our attention, and for allowing a paratype to remain in the National Museum of Natural History, Smithsonian Institution. We are also indebted to Mr. André Verhecken, Mortsel, Belgium, for comparing this new species with a paratype of *Admetula cornidei,* as well as with an undescribed northwestern African species of *Admetula.*

Literature Cited

Altimira, C. 1978. Avance sobre algunos moluscos colectados por la expedición "Atlor VII."—Resultados Expediciones Cientificas del Buque Oceanografico "Cornide de Saavedra" 7:169–171.

Cossmann, M. 1889. Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris. Quatrième Fascicule.—Annales de la Société Royal Malacologique de Belgique 23:3–381, pls. 1–12.

Petit, R. E. 1970. Notes on Cancellariidae (Mollusca: Gastropoda)–II.—Tulane Studies in Geology and Paleontology 8(2):83–88, pl. 1.

———. 1974. Notes on Japanese Cancellariidae.—Venus 33(3):109–115.

———. 1976. Notes on Cancellariidae (Mollusca: Gastropoda)–III.—Tulane Studies in Geology and Paleontology 12(1):33–43, pls. 1–2.

———, & M. G. Harasewych. 1986. New Philippine Cancellariidae (Gastropoda: Cancellariacea), with notes on the fine structure and function of the nematoglossan radula.—The Veliger 28(4): 436–443.

Smith, J. L. B., & P. C. Heemstra. 1986. Smiths' sea fishes. Southern Book Publishers, Johannesburg, xx + 1047 pp.

Solander, D. C. 1766. [descriptions of species]. *In:* G. Brander, Fossilia Hantoniensia collecta, et in Musaeo Brittannico deposita, a Gustavo Brander. Londini. vi + 43 p., 9 pls.

(REP) Research Associate, (MGH) Associate Curator, Department of Invertebrate Zoology, NHB stop 118, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 184–188

PYCNOPHYES CHUKCHIENSIS, A NEW HOMALORHAGID KINORHYNCH FROM THE ARCTIC SEA

Robert P. Higgins

Abstract.—A new species of Kinorhyncha, *Pycnophyes chukchiensis,* is described and illustrated from soft sediments of the Chukchi Sea, about 430 km northwest of Point Barrow, Alaska, at a depth of 210 m. This is the fourth member of this genus described from Arctic waters. The presence of pronounced middorsal spinous processes on all but the terminal trunk segment, the twelfth spinous process extending well beyond the terminal margin, separates this species from all congeners. Two additional unidentified species of *Pycnophyes* are noted: one from the same area as the newly described species, and one from a second general area about 160 km northwest of Point Barrow.

Between May 1960 and March 1961 the Arctic Research Laboratory Ice Station I (Drift Station Bravo, Fletcher's Ice Island) was used as a platform from which benthic samples were collected as it drifted in the Chukchi Sea northwest of Point Barrow, Alaska. Two scientists, Robert Lavenberg and John Tibbs, collected eight benthic samples at depths ranging from 38–747 m from which they extracted several specimens of the phylum Kinorhyncha. The only species described so far from this material is *Echinoderes arlis* Higgins, 1966, a member of the order Cyclorhagida. This species was based on six specimens from two samples taken about 430 km northwest of Point Barrow, at the southern limits of the Chukchi Rise. The remaining three samples from this same general area contained four specimens of the homalorhagid genus *Pycnophyes,* two of the new species described herein and two of an unidentified species. A second area, about 160 km northwest of Point Barrow, yielded an additional five specimens of this same genus but not the same species. Of these specimens, only one was in a condition suitable for the description of a new species. Because additional specimens were thought to be forthcoming but were not, this aforementioned specimen was set aside and the species it represented was not described.

Prior to 1960, only a single kinorhynch, *Echinoderes arcticus* (Steiner, 1919), had been found within the Arctic Circle. This cyclorhagid species, known only from a single specimen collected in the Barents Sea, near Murmansk, appears to be a juvenile stage of *Echinoderes* (Higgins 1983). Since the collection of the specimens from the Chukchi Sea (1960–1961), only two additional papers have described species from within the Arctic Circle. The most comprehensive study is that of Higgins & Kristensen (1988) in which five species of *Echinoderes* and two species of *Pycnophyes* are described from Disko Island, on the west coast of Greenland. More recently, two species of *Pycnophyes* were described from the Canadian coast of the Beaufort Sea (Higgins & Korczynski 1989).

Additional unidentified kinorhynchs from within the Arctic Circle have been reported by Sheremetevskij (1977) from the Laptev Sea in the vicinity of the Novosibirsk Islands, by Dinet (1977) from the Greenland

and Norwegian Seas, and by Carey & Montagna (1982) from the Alaskan coast of the Beaufort Sea. Recently, kinorhynchs have been collected by Kristensen (pers. comm.) from the Foxe Basin near Iglookik, Canada. Other unidentified Arctic Ocean kinorhynchs have been reported from Onega Bay of the White Sea (Galtsova & Sheremetevskij 1985).

Pycnophyes chukchiensis, new species
Figs. 1, 2

Diagnosis.—Trunk length 720 μm, segments nearly equal in width; lateral terminal spines 200 μm long, 28% of trunk length, tapering distally, curving mesially; four slightly emarginate dorsal, two even-margined ventral placids; subdorsal sensory seta centered about middistance from and on either side of dorsal midline on segments 4–11, lateroventral sensory setae on tergites 4–12 near tergal-sternal junction, ventral sensory seta about ⅓ distance from mesial margin of sternites 4–12 with additional sensory seta near lateral margin of sternites 7 and 12; spinous processes on segments 3–12, increasing in length posteriorly, spinous process on segment 12 extending well beyond terminal segment; ventral plates of terminal segment with lateral margins forming prominent spinous projections.

Description.—Holotypic male (author's number RH 2314.1) USNM 234448 (Figs. 1, 2), trunk length 720 μm; MSW-6 (maximum sternal width at segment 6) 84 μm, 11.7% of trunk length; SW (standard width at segment 12) 78 μm, 10.8% of trunk length.

Segment 2.—Consists of four slightly emarginate dorsal placids, 34 μm wide, and two even-margined ventral placids.

Segment 3.—Length 114 μm; with pronounced, pointed anterolateral tergal processes; slight punctate sculpturing near anterior, even margin of tergal plate; subdorsal sensory seta near anterior margin, on either side of dorsal midline, in line with junction of each lateral pair of placids; small pore mesial and slightly posterior to each subdorsal sensory seta. Midsternal plate 42 μm wide anteriorly, 80 μm wide posteriorly, lateral margins straight, with thin area adjacent to anterior margin; episternal plates with sensory spot near posteromesial margin, slight evidence of muscle scar, otherwise without distinguishing morphology.

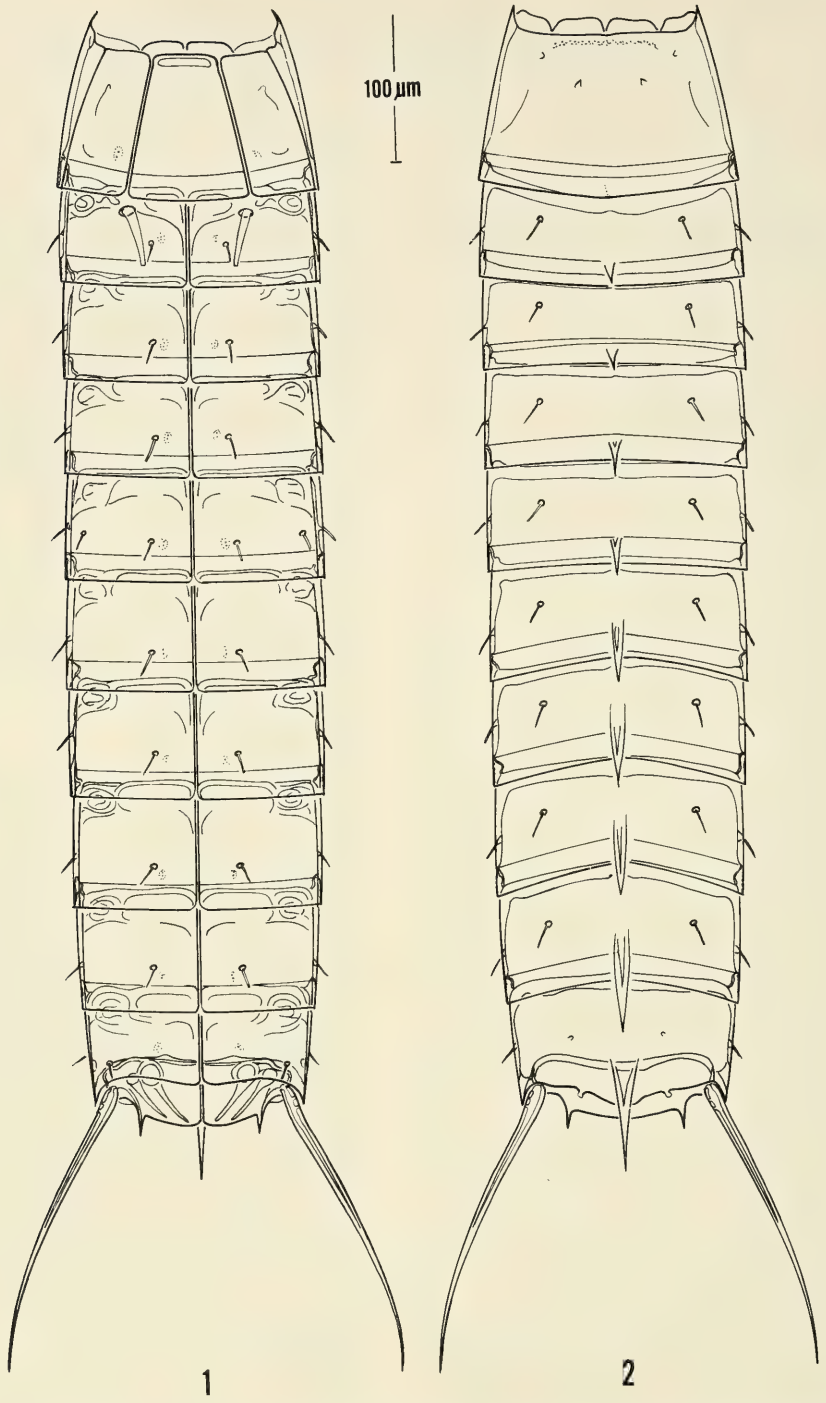
Segment 4.—Length 72 μm; pachycycli of both tergal and sternal plates well developed (Figs. 1, 2), peg-and-socket configuration prominent at junction of tergal and sternal plates; tergite with small (10 μm long) middorsal process; subdorsal sensory seta centered on each lateral surface of tergite; lateral tergal seta near tergal-sternal junction. Adhesive tubes of male, 40 μm long, near anterior margin of each sternal plate, immediately posterior to pachycyclus, in line with episternal-midsternal junction of preceding segment; sensory seta posteromesial to each adhesive tube, near arthrocorial junction; sensory spot mesial to each sensory seta.

Segment 5.—Length 71 μm; tergal plate with slightly longer middorsal process, otherwise similar to that of segment 4. Pachycycli of sternal plates less prominent, without adhesive tubes, sensory seta about ⅓ distance from ventral midline (in line with sensory seta on previous segment), otherwise similar to that of segment 4.

Segment 6.—Length 71 μm, tergal plate with slightly longer middorsal process, otherwise both tergal and sternal plates similar to those of segment 5.

Segment 7.—Length 72 μm, tergal plate with slightly longer middorsal process, mesial element of sternal pachycyclus not rounded near junction with peg-and-socket area as in previous segments; additional sensory seta near lateral margin of each sternal plate (Fig. 1).

Segment 8.—Length 78 μm, tergal plate with slightly longer middorsal process (32 μm long), without sensory seta near lateral margin of each sternal plate; otherwise similar to segment 7.



Figs. 1, 2. *Pycnophyes chukchiensis,* holotypic male (USNM 235448): 1, Neck and trunk segments, ventral view; 2, Same, dorsal view.

Segment 9.—Length 80 μm, tergal plate with slightly longer middorsal process; otherwise similar to segment 8.

Segment 10.—Length 81 μm, tergal plate with slightly longer middorsal process; mesial element of sternal pachycyclus rounded near junction with peg-and-socket area as in segments 4–6; otherwise similar to segment 9.

Segment 11.—Length 83 μm, tergal plate with slightly longer middorsal process; otherwise similar to segment 10.

Segment 12.—Length 84 μm, tergal plate with distinctly longer middorsal process (76 μm long), projecting well beyond margin of terminal segment; subdorsal sensory setae not evident; sternal plates with sensory seta near lateral margin and additional mesially adjacent sensory seta, both near arthrocorial junction; sensory spot mesial to sensory setae.

Segment 13.—Length 50 μm, tergal plate slightly rounded with minute, rounded marginal projections subdorsally; sternal plates deeply incised near lateral margins to accommodate lateral terminal spines, lateral margin of incised portion extending posteriorly, spinously projecting well beyond terminal margin. Lateral terminal spines long, 200 μm, about 8 μm thick midlength, evenly tapered, slightly recurved mesially, 28% of trunk length. Paired penile spines lateral at anterior margin of each sternal plate, anteromesial penile spine 45 μm long, broadly rounded basally; posterolateral element shorter, 40 μm long, not enlarged basally.

Material examined.—Holotypic male, TL 720 μm long (RH 2314.1) USNM 235448, from soft sediment, 210 m depth, Chukchi Sea, Arctic Ocean, 74°48′N, 167°18′W, col. R. Lavenberg and J. Tibbs, 15 Mar 1961; paratypic juvenile J-6, TL 560 μm long (RH 2310.1) USNM 235449, from soft sediment, 197 m depth, Chukchi Sea, Arctic Ocean, 74°54′N, 167°18′W, col. R. Lavenberg and J. Tibbs, 15 Mar 1961. Type material is deposited in the Invertebrate Zoology collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 (USNM).

Remarks.—Of 27 described species of *Pycnophyes,* 19 have middorsal processes ranging from minute processes on *P. ponticus* Reinhard, 1881 to the elongate processes on such species as *P. carinatus* Zelinka, 1928, *P. chiliensis* Lang, 1953, and *P. odhneri* Lang, 1949. None of these, with the exception of *P. cryopygus* Higgins & Kristensen, 1988, has a middorsal spinous process on segment 12, and, in the latter species, this process is minute or absent.

A second both obvious and unique character of *P. chukchiensis* is the elongate spinous extension of the lateral margin of the terminal sternal plates. Several species have small, usually truncate or rounded extensions at or near the laterotermínal margins of the sternal plates of segment 13, but none are as distinctive as they are on the new species. Together with the extended middorsal spinous process of segment 12, a total of three spine-like structures extend from the terminal margin of the trunk.

Pycnophyes chukchiensis is one of only seven species of this genus not having distinctive Mittelwülste. The lack of these typically oval or bean-shaped thickenings of the cuticle at or near the anteromesial margins of the sternal plates (on at least segments 11 and 12) could indicate that the single adult specimen is newly molted, but I believe this is not the case. Nonetheless, *P. cryopygus,* also from Arctic waters, shares the absence of Mittelwülste with the new species. Similarly, the presence of a sensory seta near the lateral margin of each sternal plate of segment 7 is shared by the two species. In *P. chukchiensis* as well as *P. cryopygus,* lateral sensory setae are otherwise present on the ventrolateral margins of the sternal plates of segments 4–12. The arrangement of the remaining setae of the two species is sufficiently different to clearly separate them.

Although *P. cryopygus,* like the new species, has four emarginate dorsal placids and

two even-margined ventral placids, some punctate sculpturing near the anterior tergal border of segment 3, and protruding, but blunt, processes as extensions of the lateral margin of the terminal sternites, it has a much wider midsternal plate on segment 3, shorter, more robust lateral terminal spines in addition to the distinguishing characters noted previously.

Other specimens.—From a different station in the same area where *P. chukchiensis* was collected (about 240 km northwest of Point Barrow) five additional specimens of *Pycnophyes* were found (USNM 235506–235508). Of these, four are adults (three males and one female) and one is a juvenile. None is in a condition that allows an accurate taxonomic assessment, but all have a moderately wide midsternal plate, similar to *P. chukchiensis,* but do not have the prominent middorsal spinous processes. From the second general locality where Lavenberg and Tibbs collected kinorhynchs (about 160 km northwest of Point Barrow) two specimens of *Pycnophyes* were found (USNM 235509, 235510), one adult male and a juvenile, of a second unidentified species. The latter species, like the former, cannot be properly assessed because of the poor condition of the specimens. It can be distinguished from the first of the two unidentifiable species by the presence of a very narrow midsternal plate.

Acknowledgments

I am grateful to Drs. J. L. Mohr, S. R. Geiger, and J. Tibbs for providing the material upon which this paper is based. The specimens were collected with support by contract NONR 228(19), NR 307-270 between the Office of Naval Research, Department of Defense, and the University of Southern California.

Literature Cited

Carey, A. G., Jr., & P. A. Montagna. 1982. Arctic Sea ice faunal assemblage: first approach to description and source of the underise meiofauna.—Marine Ecology Progress Series 8:1–8.

Dinet, A. 1977. Données quantitative sur le meiobenthos bathyl de la Mer de Norvège. Pp. 13–14 *in* Géochimie organique des sédiments marins profound. Orgon I. Mer de Norvège, Août 1974. CEPM-CNEXO, Comité Études Géo-Chimie Marin, CNRS, Paris.

Galtsova, V. V., S. M. Sheremetevskij. 1985. Meiobenthos of Onega Bay of the White Sea.—Issledovaniya Fauny Morei 33:88–112 [in Russian with English summary].

Higgins, R. P. 1966. *Echinoderes arlis,* a new kinorhynch from the Arctic Ocean.—Pacific Science 20:518–520.

———. 1983. The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize. II. Kinorhyncha.—Smithsonian Contributions to Marine Science 18:1–131.

———, & R. E. Korczynski. 1989. Two new species of *Pycnophyes* (Homalorhagida, Kinorhyncha) from the Canadian coast of the Beaufort Sea.—Canadian Journal of Zoology 67:2056–2064.

———, & R. M. Kristensen. 1988. Kinorhyncha from Disko Island, West Greenland.—Smithsonian Contributions to Zoology 458:1–55.

Lang, K. 1949. Echinoderida. Pp. 1–22 *in* N. H. Odhner, ed., Further zoological results of the Swedish Antarctic Expedition, 1901–1903. Volume 4, No. 2, P. A. Norstedt & Söner, Stockholm.

———. 1953. Reports of the Lund University Chile Expedition 1948–49, 9: Echinoderida.—Kungliga Fysiografiska Sällskapets Handlingar, new series 64:1–8.

Reinhard, W. 1881. Über *Echinoderes* und *Desmoscolex* der Umgegend von Odessa.—Zoologischer Anzeiger 4:588–592.

Sheremetevskij, A. M. 1977. Littoral meiobenthos in the Labtev Sea and Novosibirsk Islands.—Gidrobiologcheskii Zhurnal 13:63–70 [in Russian with English summary].

Steiner, G. 1919. Zur Kenntnis der Kinorhyncha nebst Bermerkungen über ihr Verwandschaftsverhältnis zu den Nematoden.—Zoologischer Anzeiger 50:177–187.

Zelinka, C. 1928. Monographie der Echinodera. Wilhelm Engelmann, Leipzig, iv + 396 pp.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(1), 1991, pp. 189–205

THE CHALINIDAE (PORIFERA) OF TWIN CAYS, BELIZE, AND ADJACENT WATERS

Walentina H. de Weerdt, Klaus Rützler, and Kathleen P. Smith

Abstract.—Eight species of the sponge family Chalinidae Gray (Haplosclerida, Demospongiae) are described from shallow-water habitats, primarily mangroves, of Twin Cays and Glover's Reef, Belize. Four species are new: *Haliclona mucifibrosa, H. magnifica, H. twincayensis,* and *H. pseudomolitba.* A key to the species and illustrations are provided.

The Twin Cays mangrove islands (16°49.4′N, 88°05.8′W) are situated about 3 km northwest of Carrie Bow Cay (Belize) on the southern extent of the extensive Belizean barrier reef complex (Fig. 1) (Rützler & Macintyre 1982). The islands harbor a rich sponge fauna, with a fair number of species possibly new to science. From collecting and monitoring studies by two of us (K. Rützler & K. Smith) during 1984–1989, it was determined that the sponge family Chalinidae Gray (Haplosclerida: Demospongiae) is represented by eight species, four of which are still undescribed. The goal of the present paper is to describe these four new species and to elucidate the taxonomic identity of the four species by comparison with type material. A key to the species is provided and based on characters of living and preserved specimens. One of the new species was never collected outside Belize. The other three have been found in the Florida Keys; one also in Curaçao, the Bahamas and Colombia; and one also in Guadeloupe. It seems therefore reasonable to designate paratypes from other localities than Twin Cays as well. The grouping of the species follows the classification of the Chalinidae as proposed by de Weerdt (1989). The renewed use of the family name Chalinidae instead of Haliclonidae was justified by de Weerdt (1986).

Materials and Methods

Most of the material has been collected by K. Rützler and K. Smith at Twin Cays during 1984–1986, 1988 and 1989, and by W. H. de Weerdt in December 1988. This material is housed in the collection of the National Museum of Natural History (NMNH) and catalogued under numbers of the United States National Museum (USNM). W. H. de Weerdt has had the opportunity to collect sponges from several other Caribbean localities during cruises to the Lesser Antilles in March/April and June/July 1989 on the R/V *Seward Johnson,* and during a field trip to the Florida Keys in July 1989. This material is incorporated in the sponge collections of NMNH and the Zoological Museum Amsterdam (ZMA), the Netherlands. A few specimens have also been collected by W. H. de Weerdt in Curaçao in December 1986 and are part of the ZMA collection. Type material has been examined at the Peabody Museum of Natural History, Yale University (YPM), New Haven, Connecticut, and at ZMA. The present descriptions are based on external morphological characters and the architecture of the skeleton. To study skeleton architecture and spicules, hand-cut tangential sections of the ectosome and cross sections of the choanosome have been made. Spicule sizes are

Fig. 1. Map of Belize detailing study sites at Twin Cays.

based on measurements of 25 fully-developed spicules in each specimen.

Systematic Descriptions

Order Haplosclerida Topsent
Family Chalinidae Gray
Genus *Haliclona* Grant, 1835

Species of the *fistulosa* Group

Architectural plan (Fig. 2a, b).—Choanosomal skeleton a rather dense, subisotropic reticulation, usually intercepted by many choanosomal spaces. Ectosomal skeleton of the same structure as the choanosome; ectosome usually very loosely overlaying the choanosome from which it is separated by extensive subectosomal spaces.

Haliclona mucifibrosa, new species
Figs. 2a–c, 3b, 4a, b

Type material.—Holotype, USNM 41517 (Belize, Twin Cays, Sponge Haven, 0.2 m, 26 Apr 1989, coll. K. Rützler & K. Smith). Paratypes, USNM 41521 (=ZMA 7580) (Belize, Twin Cays, Sponge Haven, NE corner, on oyster shells, 5 Jun 1984, coll. K. Rützler & K. Smith); USNM 41762 (Florida, Florida Keys, ca. 1 km NW of Menson Island, back reef flat, on sandy bottom, ca. 1 m, 13 Jul 1989, coll. W. H. de Weerdt & S. Viada); ZMA POR. 6403 (Curaçao, entrance Fuikbaai, on sandy bottom, 3 m, 13 Jan 1987, coll. W. H. de Weerdt & P. Hoetjes). Additional material, USNM 41518 (Belize, Twin Cays, Batfish Point, on

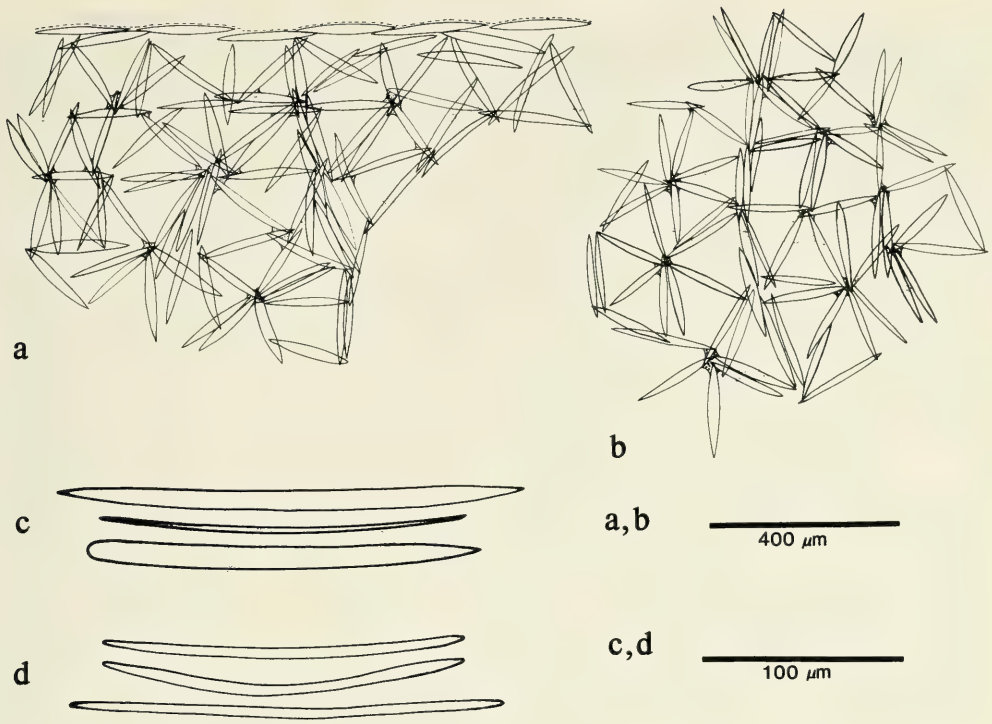


Fig. 2. Chalinidae of the *fistulosa* Group: a, Choanosomal skeleton; b, Ectosomal skeleton; c, Spicules of *Haliclona mucifibrosa*; d, Spicules of *H. magnifica*.

mangrove roots and bank, 0–1 m, 28 Apr 1986, coll. K. Smith & K. Rützler); USNM 41519 (Belize, Twin Cays, Grouper Gardens, 0.5 m, 19 Apr 1986, coll. K. Rützler & K. Smith); USNM 41520 (Belize, Twin Cays, Sponge Haven, 21 Apr 1986, associated with *Xestospongia wiedenmayeri* van Soest, coll. K. Rützler & K. Smith); Bahamas, USNM 33572 (Bahamas, Andros Island, 30 m, 1982, coll. British Cave Diving Expedition); Florida, USNM 41761 (Florida, Biscayne Bay, Jul 1948, coll. M. W. de Laubenfels; unpublished specimen, originally identified by de Laubenfels as *Haliclona*); USNM 41763 (Florida, Florida Keys, under the bridge between Ramrod Key and Little Torch Key, pillars and muddy bottom, 1–3 m, 11 Jul 1989, coll. W. H. de Weerdt & S. Viada); USNM 41764 (Florida, Florida Keys, unnamed mangrove island ca. 400 m E of Big Torch Key, on mangrove roots, 12 Jul 1989, coll. W. H. de Weerdt & S. Viada); Colombia, USNM 41832 (Colombia, Bahia Portete, Guajira peninsula, 0.5 m, on lower parts of *Millepora* on *Thalassia,* 27 Jul 1987, coll. S. Zea).

Diagnosis.—Shape: Irregularly lumpy, massive base, typically about 10 cm in diameter, from which arise short (2–3 cm), truncate, rather thick-walled oscular chimneys. Oscules to 1 cm in diameter. Lateral expansions (fistules) 10–15 cm or more.

Color: Greyish purple to bluish gray in life (Fig. 3b).

Surface: Smooth, but occasionally with tuberculate areas caused by short fistule-like projections.

Consistency: Elastic compressible but easily torn; pronounced mucus strands appear when fragments are torn apart.

Choanosomal skeleton: Subisotropic, rigid reticulation of high spicule density, spongin inconspicuous (Figs. 2a, 4a).

Ectosomal skeleton: Tangential, sub-iso-

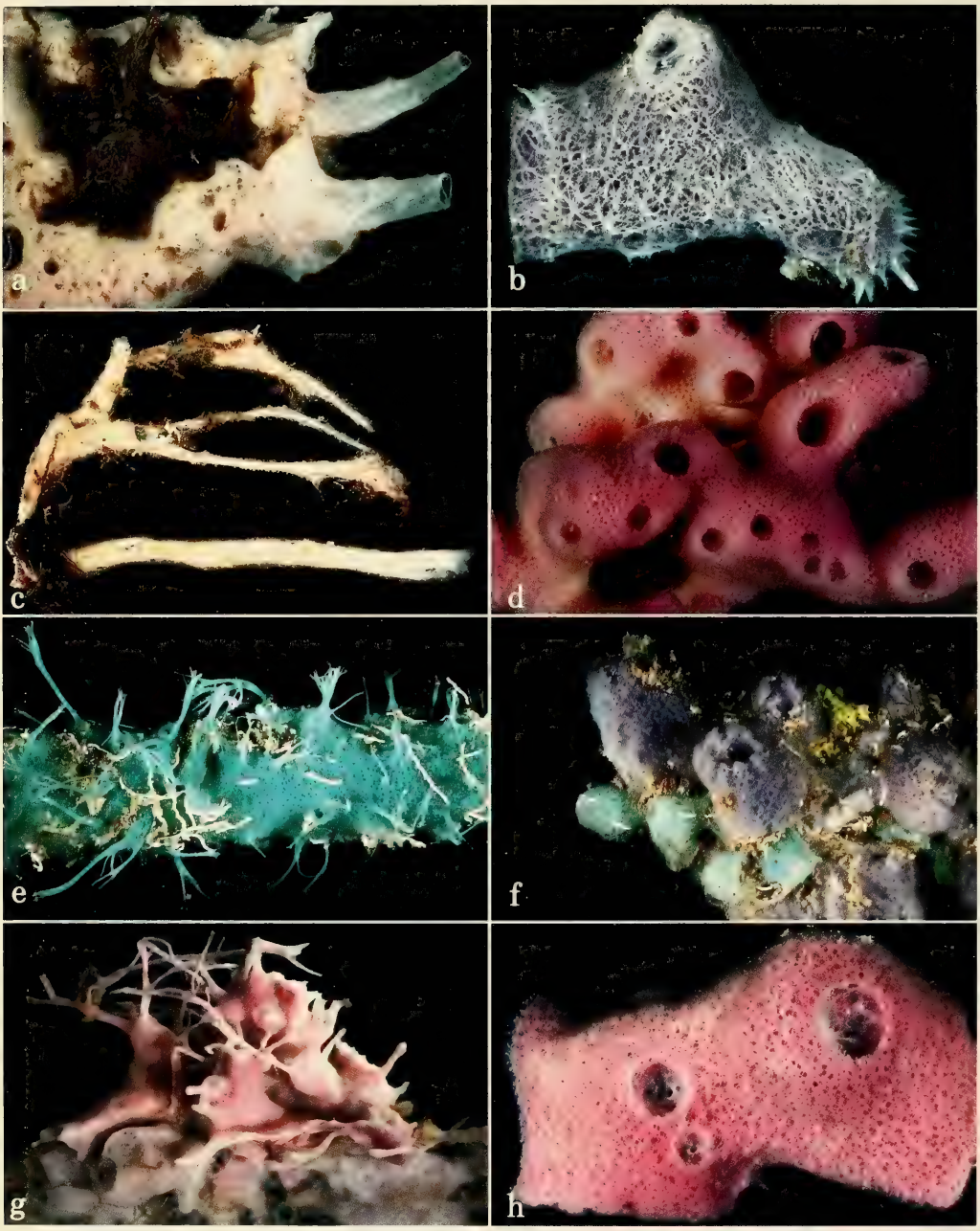


Fig. 3. Photomicrographs of live *Haliclona* specimens from Twin Cays mangroves: a, *Haliclona magnifica,* freshly dislocated from its peat substrate which is apparent at the upper left, ×0.7; b, *Haliclona mucifibrosa,* ×0.9; c, *Haliclona twincayensis,* ×0.8; d, *Haliclona pseudomolitba,* ×0.8; e, *Haliclona manglaris,* ×0.9; f, *Haliclona curacaoensis,* ×0.9; g, *Haliclona tubifera,* ×0.8; h, *Haliclona implexiformis,* ×0.9

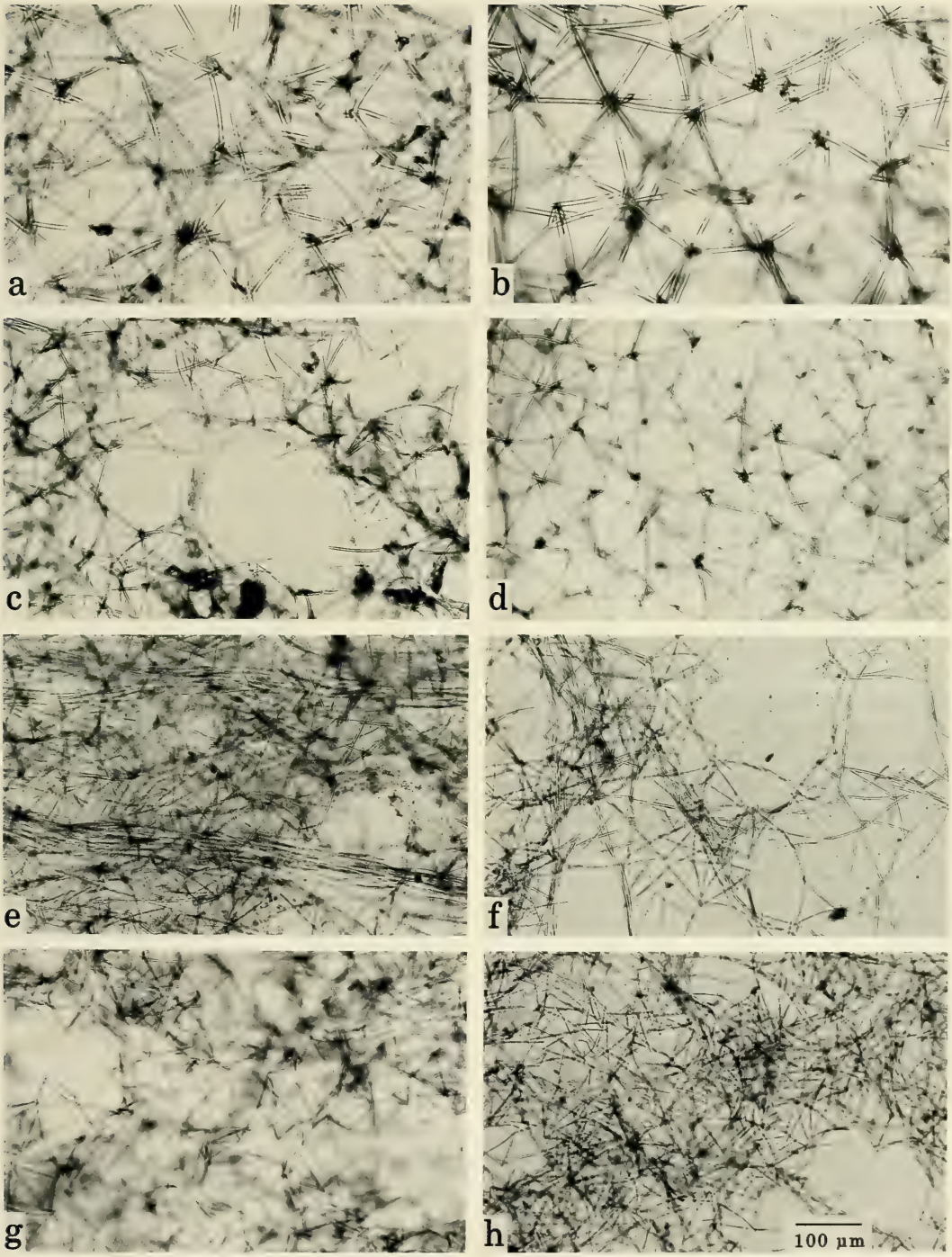


Fig. 4. Photomicrographs of holotype tissue sections from all four new species of *Haliclona*; choanosome to the left (a, c, e, g), ectosome to the right (b, d, f, h): a, b, *H. mucifibrosa*; c, d, *H. magnifica*; e, f, *H. twincayensis*; g, h, *H. pseudomolitba*. (Scale on h applies to all photomicrographs.)

Table 1.—Spicule sizes, length × width (μm), of four specimens of *Haliclona mucifibrosa* (ranges, means, standard deviations, $n = 25$).

USNM	41517	214.6–237.1 (±9.2)–250.6 × 9.3–11.7 (±1.0)–13.7
	41521	207.5–220.5 (±10.6)–237.5 × 7.0–10.7 (±2.2)–14.0
	41762	188.6–208.2 (±8.0)–220.4 × 7.4– 9.1 (±0.5)–10.0
ZMA	6403	148.5–180.5 (±14.0)–204.2 × 4.9– 6.4 (±0.7)– 7.2

tropic spicule-rich reticulation, similar to choanosomal network (Figs. 2b, 4b).

Fistule architecture: Same as ectosome and choanosome, no special reinforcement.

Spongin: Distinct, at the nodes of the spicules.

Spicules: Oxeas, straight or slightly, evenly curved, robust, with long and sharp points; occasionally the points are mucronate (Fig. 2c). Length × width (range of means for four specimens measured, Table 1): 180.5–237.1 × 6.4–11.7 μm.

Ecology.—Habitats are mangrove roots, peat banks, shallow sandy bays, and reef caves. The species is abundant on lower intertidal peat banks of Cuda Cut, Twin Cays, where specimens can become fully air-exposed during low ebb tides.

Distribution.—Belize, Curaçao, Bahamas, and Florida.

Etymology.—This species was named for heavy mucus strands that develop when fragments are torn apart.

Discussion.—*Haliclona mucifibrosa* is, to our knowledge, the only chalinid species of the *fistulosa* group that develops mucus strands. So far, this feature has only been observed in species of the *aquaeducta* group (de Weerdt 1989). Because of the mucus strands, but also because of the color and growth form, *H. mucifibrosa* may be confused with *H. tubifera* (George & Wilson). The latter species has smaller spicula (105–155 × 4.0–7.5 μm) and a very delicate, unispicular, isotropic ectosomal and choanosomal skeleton. *H. tubifera* also has a more delicate shape and a tendency to form long, thin proliferations. *H. mucifibrosa* differs from *H. magnifica,* described below, by the pronounced mucus strands and its much more robust oxeas. A third Caribbean species belonging to the *fistulosa* group is *H. albifragilis* Hechtel. This species stands out by its shape (thinly encrusting) and color (white) and occurs in cryptic habitats (under coral rubble). *Haliclona albifragilis* has not been found in Belize, but this may be due to its cryptic and apparently also rare occurrence. Specimen USNM 41832 (Colombia) stands out by the large size of its oxeas (mean length × width = 254.2 × 14.0 μm), but this feature seems to be common in sponges from certain areas of the Atlantic coast of Colombia (Zea 1987, and in litt.).

Haliclona magnifica, new species
Figs. 2a, b, d, 3a, 4c, d

Type material.—Holotype, USNM 41500 (Belize, Twin Cays, Hidden Creek, 1 m, 9 May 1985, coll. K. Smith & K. Rützler). Paratypes, USNM 41501 (Belize, Twin Cays, Batfish Point, 1 m, 19 Apr 1986, coll. K. Rützler & K. Smith); USNM 41502 (Florida, Florida Keys, unnamed mangrove island 400 m E of Big Torch Key, 13 Jul 1989, coll. W. H. de Weerdt & S. Viada); ZMA POR. 7579 (same site as USNM 41502, 12 Jul 1989, coll. W. H. de Weerdt & S. Viada). Additional material, USNM 41514 (Belize, Twin Cays, Grouper Gardens, peat bank, 0.2 m, 7 Dec 1988, coll. W. H. de Weerdt); USNM 41522 (Belize, Twin Cays, Hidden Creek, 29 Jun 1984, coll. K. Smith & K. Rützler).

Diagnosis.—Shape: Irregularly massive base from which arise one to four thick-walled tubes, to 15 cm high and 5 cm thick.

Table 2.—Spicule sizes, length × width (μm), of four specimens of *Haliclona magnifica* (ranges, means, standard deviations, $n = 25$).

USNM	41500	189.6–206.9 (±8.8)–220.6 × 3.8–5.5 (±0.5)–5.9
	41501	181.2–198.5 (±9.6)–215.8 × 4.6–5.2 (±0.3)–5.8
	41502	174.0–196.7 (±13.7)–220.4 × 5.1–6.0 (±0.5)–6.7
ZMA	7579	171.7–194.6 (±11.9)–218.1 × 4.9–5.6 (±0.6)–6.7

Each tube tapers towards an oscular chimney and osculum of 1–2 cm diameter. Characteristically, the choanosome, still present in the basal parts of the tubes, disappears towards the osculum, so that the distal part of the tubes consists of the ectosomal skeleton only. In addition, several smaller fistules, 2–5 cm thick and as much as 8 cm high, may arise at irregular distances from all parts of the sponges.

Color: Pink, to dull pink and drab, with white oscular fistules (Fig. 3a).

Surface: Smooth.

Consistency: Slightly crisp, very fragile, compressible, but not elastic; mucuous when rubbed between fingers.

Choanosomal skeleton: Regular, subisotropic reticulation dominated by spicules (Figs. 2a, 4c).

Ectosomal skeleton: Indistinguishable from choanosomal skeleton but easily detached (Figs. 2b, 4d); in addition, the ectosomal skeleton is reinforced by longitudinal spicula tracts towards the distal portions of the tubes where the choanosomal skeleton is absent.

Fistule architecture: Subisotropic, reinforced by loosely organized longitudinal spicule tracts that consist of 4–6 spicules with overlapping points.

Spongin: Scarce, confined to the nodes of the spicules.

Spicules: Oxeas, slender, fusiform, slightly flexuous (Fig. 2d). Length × width (range of means for 6 specimens, including those of Table 2): 194.6–206.9 × 5.2–6.0 μm.

Ecology.—Typical habitats are peat undercuts and banks in mangrove channels. The basal mass of specimens is typically hugging depressions in the exposed peat surface, with only the whitish oscular chimneys protruding. The species has a remarkable tolerance to sudden changes of temperature and salinity that occur in the mangrove channels with changes of tidal flow.

Distribution.—Belize, Florida, Puerto Rico.

Etymology.—The species is named *Haliclona magnifica* because of its magnificent color and shape.

Discussion.—*Haliclona magnifica* is a very characteristic species, not only for its color and growth form, but also for its slender, flexuous spicula, and confusion with other local species is hardly possible. As far as Belizean chalinids are concerned, *H. magnifica* is most closely related to *H. mucifibrosa* (see above). It differs from this species by its color and shape, the lack of pronounced mucus strands, the much thinner oxeas and scarcer spongin. *Haliclona magnifica* stands out among other species of the *fistulosa* group by its slender flexuous spicula, which is a common feature in the *arenata* and *rosea* groups (cf., de Weerdt 1989). As far as North Atlantic species are concerned, the oxeas of the *fistulosa* group are consistently robust, straight "needles." Yet, by its subisotropic skeleton and extensive subectosomal spaces, *H. magnifica* clearly belongs to the *fistulosa* group.

Species of the *arenata* Group

Architectural plan (Fig. 5a, b).—Choanosomal skeleton a rather irregular reticulation with ill-defined paucispicular primary lines which are irregularly connected by uni-

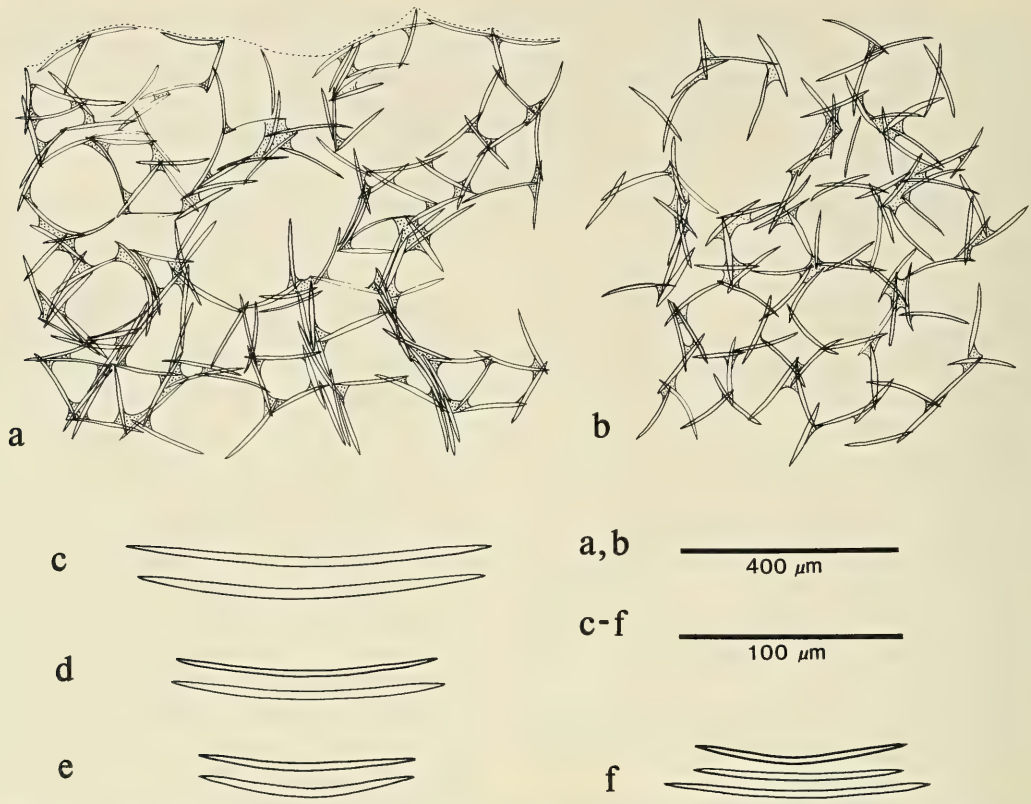


Fig. 5. Chalinidae of the *arenata* Group: a, Choanosomal skeleton; b, Ectosomal skeleton; c, Spicules of *Haliclona twincayensis*; d, Spicules of *H. pseudomolitba*; e, Spicules of *H. manglaris*; f, Spicules of *H. curacaoensis*.

spicular secondary lines. There is a vague tendency towards rounded meshes. Ectosomal skeleton, if present, a discontinuous but coherent tangential reticulation of single spicules. The tendency to form rounded meshes is more pronounced in the ectosomal skeleton than in the choanosomal skeleton. Usually, the ectosomal membrane is clearly observable with closely-packed pores in the open spaces between the spicules. Spongin is always present at the nodes of the spicules, but never abundant. Oxeas fusiform, slender, usually curved or flexuous. Microscleres sometimes present.

Haliclona twincayensis, new species
Figs. 3c, 4e, f, 5a–c

Type material.—Holotype, USNM 41515 (Belize, Twin Cays, Hidden Creek, 1.5 m, 1 May 1989, coll. K. Smith & K. Rützler). Paratypes, USNM 41289 (Belize, Twin Cays, Grouper Gardens, 0.5 m, 10 Jun 1983, coll. K. Rützler); USNM 41516 (Belize, Twin Cays, Hidden Creek, 1.5 m, 1 May 1989, coll. K. Smith & K. Rützler); USNM 41770 (Florida, Florida Keys, under the bridge between Ramrod Key and Little Torch Key, on piles, 1–3 m, 11 Jul 1989, col. W. H. de Weerdt & S. Viada); ZMA POR. 7582 (same data as USNM 41515); USNM 41771 (Guadeloupe, Grand Cul-de-Sac Marin, ca. 0.5 mi N of Petit Canal, E side Bay, 16°23.5′N, 61°30.60′W, piling off dock and old house, 0.2 m, 23 Jun 1989, coll. W. H. de Weerdt).

Diagnosis.—Shape: Slender, solid, partly fused, erect whips or branches, 2–12 mm thick, 5–10 cm long, projecting without an

Table 3.—Spicule sizes, length × width (μm), of six specimens of *Haliclona twincayensis* (ranges, means, standard deviations, $n = 25$).

USNM 41515	146.2–155.4 (±6.2)–165.9 × 4.2–4.6 (±0.3)–5.3
41516	137.5–152.8 (±10.2)–167.5 × 3.7–4.9 (±1.1)–6.2
41289	142.5–151.7 (±9.4)–162.5 × 3.5–4.4 (±0.5)–5.5
41770	141.5–162.2 (±9.3)–176.3 × 5.1–6.1 (±0.6)–7.0
41771	111.4–120.3 (±4.4)–127.6 × 4.4–4.8 (±0.3)–5.8
ZMA 7582	150.0–158.6 (±5.2)–167.5 × 3.7–4.5 (±0.5)–5.2

apparent base directly perpendicular from the substratum (mangrove roots, peat banks, piles). Oscula inconspicuous, rare, ca. 1 mm, irregularly distributed along all sides of the branches.

Color: Whitish gray to light tan in life, light tan in spirit (Fig. 3c).

Surface: Strongly punctate, with pronounced longitudinal subectosomal spaces, which are roofed by tangential ectosomal spicules.

Consistency: Rather firm, only slightly compressible, but fragile.

Choanosomal skeleton: Paucispicular primary lines connected by unispicular secondary lines, ill-defined and irregular (Figs 4e, 5a); many spicules, including numerous developmental forms, are placed in confusion.

Ectosomal skeleton: Unispicular, tangential reticulation, irregular and discontinuous (Figs. 4f, 5b); with many open spaces between the spicules.

Spongin: Scarce, confined to the nodes of the spicules.

Spicules: Oxeas, slender, fusiform, slightly flexuous (Fig. 5c). Length × width (range of means for six specimens measured, Table 3): 120.3–162.2 × 4.4–6.1 μm.

Ecology.—Habitats are stilt roots of red mangrove, peat undercuts and bank, artificial wood piling from just below tide level to 3 m depth. Fairly extreme and sudden temperature and salinity changes are tolerated in mangrove channels during changing tides.

Distribution.—Belize, Florida, Guadeloupe.

Etymology.—The species is named after its type locality, Twin Cays.

Discussion.—*Haliclona twincayensis* is related to the Caribbean species *H. caerulea* (Hechtel), *H. manglaris* Alcolado and *H. curacaoensis* (van Soest). The latter two species occur also in Belize. *H. caerulea* is distinct by its bluish gray color and the possession of sigmata. *H. manglaris* (see below) is thinly encrusting, bright turquoise green, and has much smaller oxeas (75–108 × 2–4 μm) than *H. twincayensis*. *H. curacaoensis* is distinct by its shape (close-packed oscular mounds), sticky consistency, and smaller oxeas (93.5–135 × 2.3–5.7 μm).

Haliclona pseudomolitba, new species
Figs. 3d, 4g, h, 5a, b, d

Type material.—Holotype, USNM 41743 (Belize, Twin Cays, Hidden Creek, 0.5 m, 1 May 1989, coll. K. Smith & K. Rützler). Paratypes, USNM 41503 (Belize, Twin Cays, Hidden Creek, 1 m, 10 Dec 1988, coll. W. H. de Weerdt); USNM 41797 (Martinique, Diamond Rock, 18 m, 3 Jul 1989); ZMA POR. 7595 (same data as USNM 41503). Other material, USNM 41742 (Belize, Hidden Creek, 0.5 m, 1 May 1989, coll. K. Smith & K. Rützler).

Diagnosis.—Shape: Erect, finger-shaped, partly fused branches, to 15 cm high. Oscules numerous, circular, flush with surface, 2–3 mm regularly distributed along the branches.

Color: Rich pink with yellowish cream tinges (Fig. 3d).

Surface: Even, rather smooth.

Consistency: Extremely soft, limp, highly compressible.

Choanosomal skeleton: Paucispicular primaries, unispicular secondaries (Figs. 4g,

Table 4.—Spicule sizes, length × width (μm), of four specimens of *Haliclona pseudomolitba* (ranges, means, standard deviations, $n = 25$).

USNM 41503	107.0–115.3 (±5.1)–126.1 × 3.6–4.5 (±0.5)–5.6
41742	110.0–115.7 (±5.6)–125.0 × 3.8–4.3 (±0.3)–5.0
41743	110.0–125.1 (±5.5)–133.0 × 2.5–4.0 (±1.0)–5.0
41797	111.4–124.5 (±8.6)–142.0 × 4.4–5.5 (±0.8)–7.0

5a), with many spicules placed in confusion, commonly reinforced by loosely organized spicule tracts of 3 or more spicules.

Ectosomal skeleton: Irregular, unispicular tangential reticulation (Figs. 4h, 5b); no particular specialization.

Spongin: Scarce, confined to nodes of spicules.

Spicules: Oxeas, fusiform, straight or evenly curved, occasionally the points are mucronate (Fig. 5d). Length × width (range of means for four specimens measured, Table 4): 115.3–125.1 × 4.0–5.5 μm.

Ecology.—Habitats are stilt roots of red mangrove, peat undercuts and bank. Fairly extreme and sudden temperature and salinity changes are tolerated in mangrove channels during changing tides.

Distribution.—Belize, Martinique.

Etymology.—The species is named for its similarity of habit with *Acervochalina molitba.*

Discussion.—*Haliclona pseudomolitba* appears at first to be very similar to *Acervochalina molitba* (de Laubenfels, 1949). Both are pink, finger-like, soft and limp, but the skeletons are distinctly different, *H. pseudomolitba* lacking any semblance of a spongin fiber skeleton. We acknowledge the marked variation in spicule size and amount of spongin in *Acervochalina* species (cf., van Soest 1980; de Weerdt 1986, 1989), but the lack of any intermediate form between the spongin-dominated forms of *A. molitba* as found in Bermuda (and described from Bimini, Bahamas by de Laubenfels 1949, and from Bermuda by de Laubenfels 1950) and our spicule-dominated specimens from Belize and Martinique prompted us to describe the latter material as a new species. The skeleton of *H. pseudomolitba* is closest to *H. twincayensis, H. manglaris,* and *H. curacaoensis* because it has a rather irregular reticulation with many spicules in confusion.

Haliclona manglaris Alcolado
Fig. 3e, 5a, b, e

Haliclona manglaris Alcolado, 1984:4, figs. 1B, 2A.

Material.—USNM 32960 (Belize, Twin Cays, Sponge Haven, associated with the tunicate *Distaplia bermudensis,* 25 Feb 1984, coll. I Goodbody); USNM 33581 (Belize, Twin Cays, Lair Channel, associated with *Distaplia* sp., 26 Feb 1985, coll. I. Goodbody); USNM 41737 (Belize, Twin Cays, Grouper Gardens, 19 Apr 1986, coll. K. Rützler & K. Smith); USNM 41752 (Belize, Twin Cays, The Lair, mangrove roots, 1 m, 8 Dec 1988, coll. W. H. de Weerdt); USNM 41757 (Belize, Twin Cays, Grouper Gardens, on mangrove roots, 0.3 m, 6 Dec 1988, coll. W. H. de Weerdt); USNM 41758 (Belize, Twin Cays, Hidden Creek, on mangrove roots, 0.5 m, 10 Dec 1988, coll. W. H. de Weerdt); USNM 41759 (Belize, Twin Cays, Grouper Gardens, on mangrove roots, 0.5 m, 12 Dec 1988, coll. W. H. de Weerdt).

Diagnosis.—Shape: Laterally spreading, thinly encrusting base (1–5 cm diameter) with low volcano- or chimney-shaped oscular elevations, usually not higher than 1.5 cm, and 2–5 mm thick. Oscular 0.5–2.5 mm in diameter. Commonly, thin (2–3 mm) sto-

lons branch off from the main body. Consistently occurring on mangrove roots.

Color: Bright turquoise green, drab in spirit (Fig. 3e).

Surface: Smooth, even, slightly punctate.

Consistency: Very soft, mucuous when rubbed between fingers.

Choanosomal skeleton: See architectural plan (Fig. 5a).

Ectosomal skeleton: See architectural plan (Fig. 5b), but more regular with less pronounced open spaces.

Spongin: Scarce, nodal.

Spicules: Oxeas, slender, rather strongly curved, fusiform, with marked long, very thin points (Fig. 4e). Dimensions: 75–108 × 2–4 μm.

Distribution.—Cuba (Alcolado 1984), Belize, Martinique, Florida, Grenadines, Grenada, Venezuela.

Discussion.—*Haliclona manglaris* is represented in a USNM collection by the schizotype (USNM 39225), which enabled us to confirm the identity of the species. Its name proves to be most appropriate because the species has so far only been found on roots of red mangrove, *Rhizophora mangle.* The species stands out by its bright turquoise green color.

Haliclona curacaoensis (van Soest)
Fig. 3f, 5a, b, f

Reniera curacaoensis van Soest, 1980:12, pl. I fig. 4, text-fig. 3.

Material.—USNM 41733 (Belize, Twin Cays, Hidden Creek, entrance to 30 m inside, mangrove roots and mud bank, 0–0.5 m, 28 Apr 1986, coll. K. Smith & K. Rützler); USNM 41734 (Belize, Hidden Creek, Twin Cays, mangrove roots, 0–0.5 m, 29 Jun 1984, coll. K. Smith & K. Rützler); USNM 41735 (Belize, Twin Cays, Hidden Creek, mangrove roots, 9 May 1985, coll. K. Rützler & K. Smith); USNM 41745 (Belize, Twin Cays, Grouper Gardens, 0.3 m, 1 May 1989, coll. K. Rützler & K. Smith); USNM 41755 (Belize, Twin Cays, Hidden Creek, on mangrove root, 0.5 m, 10 Dec 1988, coll. W. H. de Weerdt); USNM 41756 (Belize, Twin Cays, Sponge Haven, on mangrove roots, 1 m, 8 Dec 1988, coll. W. H. de Weerdt); USNM 41760 (Belize, Twin Cays, Grouper Gardens, on mangrove roots, 6 Dec 1988, coll. W. H. de Weerdt); USNM 41768 (Belize, Twin Cays, Gator Creek, 30 Jun 1984, coll. K. Smith & K. Rützler).

Diagnosis.—Shape: Rather close-packed, low oscular mounds, 2–3 cm thick at the basis, gradually diminishing in size towards the distal parts, 2–4 cm high; occasionally encrusting. Oscula about 3 mm in diameter.

Color: Purple, greyish purple to blue gray in life, drab in spirit. (Fig. 3f).

Surface: Smooth, but strongly punctate; commonly beset by calcareous (serpulid) worm tubes.

Consistency: Soft, sticky to the touch, mucuous when rubbed.

Choanosomal skeleton: See architectural plan (Fig. 5a), but with wavy paucispicular primary lines.

Ectosomal skeleton: See architectural plan (Fig. 5b), but less coherent.

Spongin: Very scarce, confined to the nodes of the spicules.

Spicules: Oxeas, very slender, fusiform, with long, thin points (Fig. 5f). Dimensions: 93.5–135.0 × 2.3–5.7 μm.

Distribution.—Curaçao (van Soest 1980), Belize, Grenada, Florida, Martinique.

Discussion.—The identity of our material with *Haliclona curacaoensis* could be firmly established through study of the holotype in the ZMA (POR. 3662). Van Soest (1980) did not mention the sticky surface, but otherwise his description fits very well with our specimens. Our records are the first since van Soest's description of the species, which was based on specimens from Curaçao. *H. curacaoensis* is distinguished from other Caribbean species with the same characteristic skeletal architecture by its compressed form, soft consistency, and grayish purple

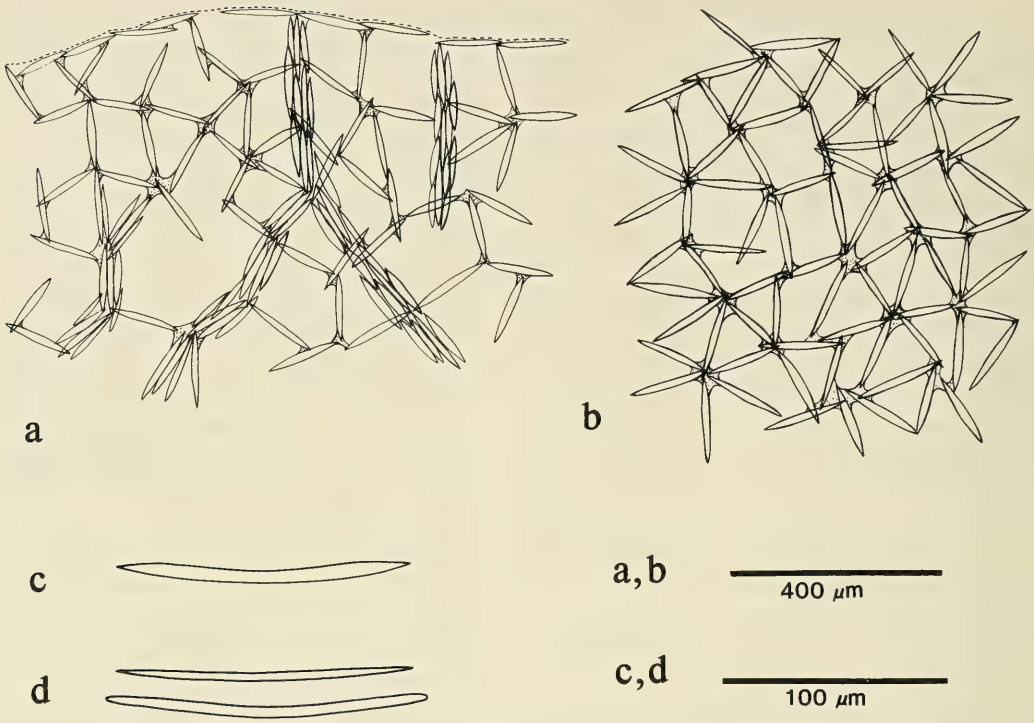


Fig. 6. Chalinidae of the *aquaeducta* Group: a, Choanosomal skeleton; b, Ectosomal skeleton; c, Spicules of *Haliclona tubifera*; d, Spicules of *H. implexiformis*.

color. The spicula are similar to those of *H. manglaris* but less strongly curved.

Species of the *aquaeducta* Group

Architectural plan (Fig. 6a, b).—Choanosomal skeleton a very regular, isotropic unispicular reticulation. Ectosomal skeleton, if present, of the same structure as the choanosomal skeleton. Spongin always present at the nodes of the spicules, but never very abundant. Spicules of variable size and form; many species have strongyles or blunt pointed oxeas as megascleres. Microscleres sometimes present.

Haliclona tubifera (George & Wilson), new combination
Figs. 3g, 6a–c

Reniera tubifera George & Wilson, 1919: 145; pl. LVII, fig. 12; pl. LVIII, fig. 15; pl. LIX, fig. 16; pl. LXVI, fig. 55a–c. *Haliclona hogarthi* Hechtel, 1965:20; pl. II, fig. 1; text-fig. 1.

Material.—USNM 32383 (Belize, Glover's Reef, SW fore reef, turtle grass, 10 m, Jul 1977, coll. J. Faulkner); USNM 34632 (Belize, Twin Cays, 24 May 1985, coll. I. Goodbody); USNM 41729 (Belize, Twin Cays, main channel near dock, *Rhizophora* roots, 26 Apr 1986, coll. K. Rützler & K. Smith); USNM 41730 (Belize, Twin Cays, Lair Channel near Lair, in undercuts, 11 May 1985, coll. K. Smith & K. Rützler); USNM 41731, USNM 41732 (same data as USNM 41729); USNM 41736 (Belize, Twin Cays, Hidden Creek, mangrove roots, 29 Jun 1984, coll. K. Rützler & K. Smith); USNM 41739, USNM 41740 (Belize, Twin Cays, Grouper Gardens, 0.2 m, 22 Apr 1989, coll. K. Rützler & K. Smith); USNM 41744

(Belize, Twin Cays, Gator Creek, 0.3 m, 3 May 1989, coll. K. Rützler & K. Smith); USNM 41746 (Belize, Twin Cays, Grouper Gardens, mangrove roots, 0.4 m, 6 Dec 1988, coll. W. H. de Weerdt); USNM 41750, USNM 41751 (Belize, Twin Cays, Sponge Haven, mangrove roots, 1 m, 8 Dec 1988, coll. W. H. de Weerdt); USNM 41754 (Belize, Twin Cays, Hidden Creek, mangrove roots, 0.5 m, 10 Dec 1988, coll. W. H. de Weerdt); USNM 41767 (Belize, Batfish Point, Twin Cays, 0–2 m, 20 Apr 1986, coll. K. Smith & K. Rützler); USNM 41773 (Belize, Twin Cays, Hidden Creek, 0.2 m, 23 Apr 1989, coll. K. Smith & K. Rützler).

Diagnosis.—Shape: Very variable; commonly a thickly encrusting or cushion-shaped base with numerous volcano- or chimney-shaped oscular elevations and rope-like stolons. The chimneys may be very pronounced and reach a height of 5 cm or more. Size of the oscula is very variable, from 1 mm to over 10 mm. The sponges have a marked tendency to form laterally spreading masses of infinite size, leaving the substratum (e.g., mangrove roots), to which they are basically attached. Other specimens may remain small, thinly encrusting or delicately branched, with irregularly distributed, small (1–2 mm), oscula which are flush with the surface or with slightly raised collars. In addition, long, thin, irregularly fused, rope-like stolons commonly branch off from the main body. These stolons may form large masses of 60 cm or more, especially when the main body is of considerable size too, but also in smaller specimens there is a tendency towards the forming of these proliferations.

Color: Bluish purple, purple, pink, purplish gray, whitish to cream in life, light tan in spirit (Fig. 3g).

Surface: Smooth, slightly punctate.

Consistency: Soft, elastic compressible, but fragile; mucuous when rubbed, mucus strands appear when sponge is squeezed or pulled apart.

Choanosomal skeleton: See architectural plan (Fig. 6a); skeleton commonly reinforced by short, loosely organized spicule tracts of 3–6 spicules.

Ectosomal skeleton: See architectural plan (Fig. 6b); the skeleton occasionally superimposed on subectosomal tangentially oriented tracts of 8–10 spicules which have their points laying abreast.

Spongin: Usually confined to the nodes of the spicules, but occasionally more abundant.

Spicules: Oxeas, sharply pointed, hastate, commonly thinner in the middle than near the ends (Fig. 6c). Dimensions: 105–155 × 4.0–7.5 μm.

Ecology.—Habitats include mangrove roots and peat banks, seagrass meadows, shallow sandy bays and fore reefs. Depth range from very shallow to ca. 10 m.

Distribution.—North Carolina (George & Wilson 1919, as *Reniera tubifera*), Jamaica (Hechtel 1965, as *Haliclona hogarthi*), Belize, Curaçao, Bonaire, Aruba, La Desirade, Florida (van Soest 1980, as *H. hogarthi*), South Carolina, Bahamas, Bermuda, Nigeria, Venezuela, Colombia, Martinique, Antigua, Grenada.

Discussion.—*Haliclona hogarthi* is here synonymized with *Reniera tubifera* on the basis of study of both the specimen of *H. tubifera* described by Wells et al. 1960 (USNM 23610; no holotype designation by George & Wilson 1919) and the holotype of *H. hogarthi* (YPM 5033). Of all the purple chalinids occurring in Belize, *H. tubifera* is, in the living state, most easily confused with *H. mucifibrosa,* yet is otherwise most closely related to *H. implexiformis* (Hechtel). The color and form of *H. tubifera* and *H. mucifibrosa* are quite similar, but *H. tubifera* has generally a more delicate habit and consistency and the proliferations (although not always present) of *H. tubifera* seem to be consistently absent in *H. mucifibrosa.* Both species have mucus strands but they are much less pronounced in *H. tubifera.* The two species may, therefore, be difficult to separate in the field, but microscopic char-

acters distinguish them immediately. The most distinguishing feature is the delicate unispicular skeleton of *H. tubifera,* which is intermittently reinforced by short spicule tracts but lacks conspicuous choanosomal spaces. *H. mucifibrosa,* on the other hand, has a rather dense, subisotropic although regular, choanosomal skeleton with many choanosomal spaces. Furthermore, the spicula of *H. tubifera* are of much smaller size than those of *H. mucifibrosa* (150–220 × 5.0–13.5 μm). The latter species has been assigned to the *fistulosa* group (see above). *Haliclona tubifera* differs from *H. implexiformis* by its more irregular form with proliferations, mucus strands, its bluish purple color, and the hastate shape of its oxeas (strongylote in *H. implexiformis*).

Haliclona implexiformis (Hechtel)
Figs. 3h, 6a, b, d

Adocia implexiformis Hechtel, 1965:27, pl. II, fig. 2, text-fig. 2. For further synonymy see van Soest (1980).

Material.—USNM 41523 (Belize, Twin Cays, Lair Channel, near Lair, undercuts, 11 May 1985, coll. K. Rützler & K. Smith); USNM 41524 (Belize, Twin Cays, Hidden Creek, entrance to 30 m inside, mangrove roots and mud bank, 0.0–0.5 m, 28 Apr 1986, coll. K. Smith & K. Rützler); USNM 41525 (Belize, Twin Cays, Sponge Haven, mangrove roots, 0.5 m, 8 Dec 1988, coll. W. H. de Weerdt); USNM 41726 (Belize, Twin Cays, Hidden Creek, mangrove roots, 0.5 m, 12 Dec 1988, coll. W. H. de Weerdt); USNM 41728 (Belize, Twin Cays, Grouper Gardens, 19 Apr 1986, coll. K. Rützler & K. Smith); USNM 41741 (Belize, Hidden Creek, Twin Cays, 1 May 1989, coll. K. Smith & K. Rützler); USNM 41748 (Belize, Twin Cays, Grouper Gardens, on mangrove roots, 0.5 m, 7 Dec 1988, coll. W. H. de Weerdt); USNM 41749 (Belize, Twin Cays, Grouper Gardens, mangrove roots, 0.5 m, 7 Dec 1988, coll. W. H. de Weerdt); USNM 41753 (Belize, Twin Cays, The Lair, on mangrove roots, 1 m, 8 Dec 1988, coll. W. H. de Weerdt).

Diagnosis.—Shape: Thick (2–4 cm) cushions, with a well-defined, although somewhat irregular outline. Oscula conspicuous, circular, rather large (6–10 mm), regularly distributed, usually flush with the surface, but also on slightly elevated mounds.

Color: Pinkish violet in life, occasionally cream, light tan in spirit; pigment can be easily squeezed out, leaving tan skeleton behind (Fig. 3h).

Surface: Usually even and smooth, rarely with tuberculate areas, rather strongly punctate.

Consistency: Soft, compressible; no obvious mucus, only slippery exudate when squeezed.

Choanosomal skeleton: See architectural plan (Fig. 6a).

Ectosomal skeleton: See architectural plan (Fig. 6b); easily detachable.

Spongin: Scarce but clearly visible, confined to the nodes of the spicules.

Spicules: Oxeas, slightly, evenly curved, with blunt points (strongylote) (Fig. 6d). Dimensions: 110–150 × 4.5–7.5 μm.

Distribution.—Jamaica (Hechtel 1965), Belize, Curaçao, Bonaire, Puerto Rico (van Soest 1980), Florida, Bahamas, St. Thomas, Dominican Republic, Guadeloupe, Martinique, Barbuda, Margarita.

Discussion.—*Haliclona implexiformis* differs from *H. tubifera* by its violet-pink color, lack of mucus strands, the more regular form, its lack of proliferating outgrowths, and the form of its oxeas. The species has caused much confusion in the literature, and quite a few records under the names of *Adocia* (=*Haliclona*) *neens* (Topsent) and *Haliclona permollis* (Bowerbank) (e.g., de Laubenfels 1936, Little 1963) are referable to *H. implexiformis.* Study of the holotype in the YPM (YPM 5034) has shown that this species is definitely not conspecific with *H. neens* nor with *H. permollis. Haliclona neens* is a valid northeastern Atlantic species (cf., de Weerdt & van Soest 1986);

H. permollis is a synonym of *H. cinerea* (Grant) (cf. de Weerdt 1986).

Key to the Species

1a. Sponges bright turquoise green. Soft, encrusting on mangrove roots, with low oscular mounds or chimneys or with small (1–2 mm) oscula flush with the surface; choanosomal skeleton consisting of ill-defined paucispicular primary lines, irregularly connected by unispicular secondary lines; ectosomal skeleton an irregular discontinuous, tangential, unispicular reticulation; spongin scarce; oxeas slender, rather strongly curved, with long points, 75–108 × 2–4 μm ..... *Haliclona manglaris*

b. Sponges brown, purple, pink, violet, bluish gray, or of unknown color; choanosomal skeleton consisting of ill-defined paucispicular primary lines, irregularly connected by unispicular secondary lines, or more regular, unispicular, isotropic or subisotropic; ectosomal skeleton an irregular discontinuous, tangential unispicular reticulation or very regular, isotropic or subisotropic; spongin scarce or more abundant; oxeas slender, fusiform, hastate, strongylote or robust needles 2

2a. Sponges delicately pink with drab tinges, extremely soft and limp, immediately collapsing when removed from the water. Finger-shaped with partly fused branches, oscula flush, circular, regularly distributed at all sides of the branches; choanosomal skeleton a delicate, rather irregular reticulation with ill-defined primary and secondary lines; ectosomal skeleton an irregular discontinuous, tangential, unispicular reticulation; spongin scarce, confined to the nodes of the spicules; oxeas fusiform, 115–125 × 4–6 μm .. .. *H. pseudomolitba*

b. Sponge not pink, not limp, not collapsing outside water 3

3a. Sponges sticky to the touch, even, although much less so, after preservation in spirit. Bluish gray; habit of pronounced closely-packed oscular mounds without a laterally spreading encrusting base; choanosomal skeleton consisting of ill-defined, paucispicular, primary lines, irregularly connected by unispicular secondary lines; ectosomal skeleton an irregular discontinuous, tangential, unispicular reticulation; spongin scarce; oxeas fusiform, 94–135 × 2–6 μm ..... *H. curacaoensis*

b. Sponges not sticky to the touch, although mucus strands may be present when the sponge is torn apart 4

4a. Mucus strands clearly present when sponge is torn apart 5

b. No mucus strands, or not observable because the sponges are preserved 6

5a. Sponges bluish purple, purplish brown or brown; forming a thickly encrusting base with volcano- or chimney-shaped oscular elevations, or thinly encrusting throughout, commonly with long, slender, irregularly fused ropy proliferations; skeleton of both the choanosome and ectosome a very delicate, unispicular, isotropic reticulation with low number of spicules, but intermittently reinforced by short spicule tracts; spongin usually confined to the nodes of the spicules, sometimes more abundant; oxeas hastate, with sharp points, usually slightly

thinner in the center than near the ends, 105–155 × 4–8 μm ..... *H. tubifera*

b. Sponges grayish purple or bluish gray; forming a thickly encrusting base with pronounced, truncate oscular chimneys, without ropy proliferations; skeleton a subisotropic, rather rigid reticulation with high spicule density, spongin distinctly present at the nodes of the spicules; oxeas robust needles, 149–251 × 5–14 μm ..... *H. mucifibrosa*

6a. Choanosomal skeleton rather irregular, with ill-defined primary lines; ectosomal skeleton a rather irregular, discontinuous, unispicular, tangential reticulation 7

b. Choanosomal and ectosomal skeletons more regular, unispicular, isotropic or subisotropic; ectosome easily detachable 8

7a. Slender branches, directly projecting from the substratum without conspicuous oscula; color whitish to light brown; spongin scarce; oxeas slender, fusiform, slightly sinuous, 111–176 × 5–7 μm ..... *H. twincayensis*

b. Thinly encrusting, with low oscular chimneys or with small (1–2 mm) oscula flush with the surface; color bright turquoise-green; oxeas slender, rather strongly curved, fusiform, with long, thin points, 75–108 × 2–4 μm ..... *H. manglaris*

8a. Skeleton very regular, isotropic, delicate, unispicular, with low spicule density 9

b. Skeleton regular but subisotropic, with high spicule density, many choanosomal spaces 10

9a. Oxeas hastate, sharp-pointed, slightly thinner in the middle than near the ends, 105–155 × 4–8 μm ..... *H. tubifera*

b. Sponge pinkish violet; thick cushions with conspicuous, rather large (6–10 mm), circular, regularly distributed oscula; soft; oxeas blunt-pointed or strongylote, 110–150 × 5–8 ..... *H. implexiformis*

10a. Sponge pink, dull pink or drab, forming an irregularly massive base from which arise one to four thick-walled tubes and several smaller fistules; slightly crisp, very fragile; oscular tubes and fistules reinforced by spicule tracts, especially towards the distal ends; oxeas flexuous, slender, 172–221 × 4–7 μm ..... *H. magnifica*

b. No tubular structures; oxeas robust needles, straight or slightly, evenly curved, 149–215 × 5–14 μm ..... *H. mucifibrosa*

Discussion

The Twin Cays mangrove islands in Belize harbor a very rich chalinid sponge fauna, as compared to mangrove communities in other Caribbean localities. Only the Florida Keys are found to have a comparably high chalinid species diversity. These two localities are not only comparable in the composition of Chalinidae species but also in the apparent absence of species that we found common in similar habitats elsewhere in the Caribbean region. An example is *Haliclona caerulea* (Hechtel), which occurs in great abundance in Curaçao, Bonaire, the Lesser Antilles and the Bahamas, but is absent from the Belizean and Florida Key mangroves.

Acknowledgments

This research was made possible by a Postdoctoral Fellowship from the Smithsonian Institution to W. H. de Weerdt. Field work in Belize was supported by the Caribbean Coral Reef Ecosystems program (CCRE) of the National Museum of Natural History, aided by a grant from the EXXON

Corporation (Contribution no. 294). Field work in the Florida Keys and the Lesser Antilles was funded by the Harbor Branch Oceanographic Institution, Florida; W. H. de Weerdt thanks S. A. Pomponi (HBOI) for logistical support. We thank W. D. Hartman (Peabody Museum of Natural History, Yale University) and R. W. M. van Soest (Institute of Taxonomic Zoology, University of Amsterdam) for the loan of type specimens. We are also indebted to M. K. Ryan for help in preparing the map and the color plate and to B. Alvarez for photographic printing.

Literature Cited

Alcolado, P. M. 1984. Nuevas especies de esponjas encontrada en Cuba.—Poeyana 271:1–22.

George, W. C., & H. V. Wilson. 1919. Sponges of Beaufort (N.C.) Harbor and vicinity.—Bulletin of the Bureau of Fisheries 36:130–179.

Grant, R. E. 1835. Animal kingdom. Pp. 107–118 *in* R. B. Todd, ed., The cyclopedia of anatomy and physiology, Vol. 1. Sherwood, Gilbert and Piper, London.

Hechtel, G. J. 1965. A systematic study of the Demospongiae of Port Royal, Jamaica.—Bulletin, Peabody Museum of Natural History 20:1–94.

Laubenfels, M. W. de. 1936. A discussion of the sponge fauna of the Dry Tortugas in particular, and the West Indies in general, with material for a revision of the families and orders of the Porifera.—Papers from the Tortugas Laboratory 30: 1–225.

———. 1949. Sponges of the Western Bahamas.—American Museum Novitates 1431:1–25.

———. 1950. The Porifera of the Bermuda Archipelago.—Transactions of the Zoological Society of London 27:1–154.

Little, F. J. 1963. The sponge fauna of the St. George's Sound, Apalachee Bay, and Panama City regions of the Florida Gulf Coast.—Tulane Studies in Zoology 11:31–71.

Rützler, K., & I. G. Macintyre. 1982. The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. Pp. 9–45 *in* K. Rützler and I. G. Macintyre, eds., The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I: Structure and communities.—Smithsonian Contribution to the Marine Sciences 12. Smithsonian Institution Press, City of Washington, 539 pp.

Soest, R. W. M. van. 1980. Marine sponges from Curaçao and other Caribbean localities. Part II: Haplosclerida.—Studies on the Fauna Curaçao and Other Caribbean Islands 62(104):1–174.

Weerdt, W. H. de. 1986. A systematic revision of the north-eastern Atlantic shallow-water Haplosclerida (Porifera, Demospongiae), part II: Chalinidae.—Beaufortia 36:81–165.

———. 1989. Phylogeny and vicariance biogeography of North Atlantic Chalinidae (Haplosclerida, Demospongiae).—Beaufortia 39:55–88.

———, & R. W. M. van Soest. 1986. Marine shallow-water Haplosclerida (Porifera) from the southeastern part of the North Atlantic Ocean.—Zoologische Verhandelingen 225:1–49.

Zea, S. 1987. Espongias del Caribeo Colombiano. Catalago Cientifico, Colciencias, Bogota, 286 pp.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

% BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD
01-938 9387

Applications published in the *Bulletin of Zoological Nomenclature*

The following applications were published on 28 September 1990 in Vol. 47, Part 3 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD.

Case No.

2734 *Thalassochernes* Beier, 1940 (Arachnida, Pseudoscorpionida): proposed designation of *Chelifer taierensis* With, 1907 as the type species.

2728 *Artemia franciscana* Kellogg, 1906 (Crustacea, Branchiopoda): proposed conservation of the specific name.

2720 *Dalla* Mabille, 1904 (Insecta, Lepidoptera): proposed conservation.

2712 *Calliphora vicina* Robineau-Desvoidy, 1830 (Insecta, Diptera): proposed conservation of the specific name.

2722 *Rivulus marmoratus* Poey, 1880 (Osteichthyes, Cyprinodontiformes): proposed conservation of the specific name.

2727 *Coccyzus euleri* Cabanis, 1873 (Aves, Cuculiformes): proposed conservation of the specific name.

2723 *Phororhacos* Ameghino, 1889 (Aves, Gruiformes): proposed conservation.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 28 September 1990 in Vol. 47, Part 3 of the *Bulletin of Zoological Nomenclature.*

Opinion No.

1608 *Marssonopora* Lang, 1914 (Bryozoa, Cheilostomata): *Membranipora densispina* Levinsen, 1925 designated as the type species.

1609 *Drepanites* Mojsisovics, 1893 and *Hyphoplites* Spath, 1922 (Mollusca, Ammonoidea): conserved.

1610 *Valanginites* Sayn in Kilian, 1910 (Mollusca, Ammonoidea): authorship of the genus confirmed, and *Ammonites nucleus* Roemer, 1841 confirmed as the type species.

1611 *Heliophanus kochii* Simon, 1868 (Arachnida, Araneae): specific name conserved.

1612 *Attus penicillatus* Simon, 1875 (currently *Sitticus penicillatus*; Arachnida, Araneae): specific name conserved.

1613 *Lucicutia* Giesbrecht in Giesbrecht & Schmeil, 1898: conserved, and *Pseudaugaptilus longiremis* Sars, 1907: specific name conserved (both Crustacea, Copepoda).

1614 *Trapezia* Latreille, 1828 (Crustacea, Decapoda): conserved.

1615 TRAPEZIIDAE Miers, 1886 (Crustacea, Decapoda) and TRAPEZIIDAE Lamy, 1920 (Mollusca, Bivalvia): homonymy removed

1616 *Ptochus* Schönherr, 1826 (Insecta, Coleoptera): *Ptochus porcellus* Boheman in Schönherr, 1834 confirmed as the type species.

1617 *Rosema* Walker, 1855 (Insecta, Lepidoptera): given precedence over *Zelica* Hübner, [1825] and *Rhogalia* Hübner, [1825].

1618 *Protocalliphora* Hough, 1899 (Insecta, Diptera) and its type species *Musca azurea* Fallén, 1817: usage conserved by the designation of a replacement lectotype.

1619 *Euribia jaceana* Hering, 1935 (currently *Urophora jaceana*; Insecta Diptera): specific name given precedence over *Euribia conyzae* Hering, 1933.

1620 *Monograptus exiguus* (Graptolithina): accepted usage conserved by citation of Lapworth (1876) as author.

1621 *Osteoglossum* Cuvier, 1829 (Osteichthyes, Osteoglossiformes): *Osteoglossum bicirrhosum* Cuvier, 1829 designated as the type species.

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON" a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Apendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

Proofs.—Authors will receive first proofs and original manuscript for correction and approval. Both must be returned within 48 hours to the Editor. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, **changes in proofs ($3.00 per change or revision),** and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

CONTENTS

Annotated catalogue of California Tertiary paleobotanical types transferred to University of California Museum of Paleontology — George L. Kennedy and Howard E. Schorn — 1

The karyotypes of the Chilean frogs *Eupsophus emiliopugini* and *E. vertebralis* (Amphibia: Anura: Leptodactylidae) — J. Ramón Formas — 7

The genus *Schizodon* (Teleostei: Ostariophysi: Anostomidae) in Venezuela, a reappraisal — Richard P. Vari and Sandra J. Raredon — 12

Platycephalus chauliodous, a new flathead fish from the eastern Indian Ocean (Teleostei: Platycephalidae) — Leslie W. Knapp — 23

On *Paracalocaris sagamiensis,* a new genus and species from Japan (Decapoda: Thalassinidea: Axiidae) — Katsushi Sakai — 30

Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) of the northwest Atlantic. II. *Periclimenes patae,* new species, a gorgonian associate from shallow reef areas off the Turks and Caicos Islands and Florida Keys — Richard W. Heard and Stephen Spotte — 40

Upogebia spinistipula, a new burrowing shrimp from the Florida shelf, northeastern Gulf of Mexico (Decapoda: Thalassinidea: Upogebiidae) — Austin B. Williams and Richard W. Heard — 49

A new troglobitic crayfish, *Procambarus (Lonnbergius) morrisi,* (Decapoda: Cambaridae) from Florida — Horton H. Hobbs, Jr. and Richard Franz — 55

Additional records of entocytherid ostracods infesting burrowing crayfishes, with descriptions of five new species — Horton H. Hobbs, Jr. and Daniel J. Peters — 64

Redescription of two species of *Pseudiphimediella* from the Southern Ocean (Amphipoda: Iphimediidae) — C. O. Coleman and J. L. Barnard — 76

A new species of caprellid associated with hydroids from southern Japan (Crustacea: Amphipoda: Caprellidae) — Masakazu Aoki — 91

Photis trapherus, a new elephantine species from the Caribbean Sea (Crustacea: Amphipoda) — James Darwin Thomas and J. L. Barnard — 96

Copepoda associated with the scleractinian coral genus *Montipora* in the Indo-Pacific — Arthur G. Humes — 101

Pynogonida of the western Pacific islands, IX. A shallow-water Guam survey, 1984 — C. Allan Child — 138

Trichobranchidae (Polychaeta) from shallow warm water areas in the western Atlantic Ocean — Vivianne Solis-Weiss, Kristian Fauchald, and Arno Blankensteyn — 147

Nicomache ohtai, new species (Polychaeta: Maldanidae) collected from the Hatsushima cold-seep in Sagami Bay — Tomoyuki Miura and Jun Hashimoto — 159

Two new branchiate scale-worms (Polynoidae: Polychaeta) from the hydrothermal vent of the Okinawa Trough and the volcanic seamount off Chichijima Island — Tomoyuki Miura and Jun Hashimoto — 166

A new species of *Hesiocaeca* (Polychaeta: Hesionidae) from hydrothermal vents at the Mariana back-arc basin with notes on other polychaetes — James A. Blake — 175

A new *Admetula* (Gastropoda: Cancellariidae) from South Africa — Richard E. Petit and M. G. Harasewych — 181

Pycnophyes chukchiensis, a new homalorhagid kinorhynch from the Arctic Sea — Robert P. Higgins — 184

The Chalinidae (Porifera) of Twin Cays, Belize, and adjacent waters — Walentina H. de Weerdt, Klaus Rützler, and Kathleen P. Smith — 189

International Commission on Zoological Nomenclature: Applications and Opinions — 206

QH
1
34x
NH

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

VOLUME 104 NUMBER 2
18 JUNE 1991
ISSN 0006-324X

THE BIOLOGICAL SOCIETY OF WASHINGTON

1990–1991

Officers

President: Leslie W. Knapp
President-elect: Storrs L. Olson
Secretary: G. David Johnson
Treasurer: Michael Vecchione

Elected Council

Roger F. Cressey, Jr.
Janet R. Gomon
Robert Hershler
Janet W. Reid
Wayne C. Starnes
Jeffery T. Williams

Custodian of Publications: Austin B. Williams

PROCEEDINGS

Editor: C. Brian Robbins

Associate Editors

Classical Languages: George C. Steyskal

Plants: David B. Lellinger
Insects: Wayne N. Mathis

Invertebrates: Stephen D. Cairns
Frank D. Ferrari
Rafael Lemaitre
Vertebrates: G. David Johnson

Membership in the Society is open to anyone who wishes to join. There are no prerequisites. Annual dues of $15.00 ($20.00 to non-USA addresses) include subscription to the *Proceedings of the Biological Society of Washington.* Library subscriptions to the *Proceedings* are: $25.00 within the U.S.A., $30.00 elsewhere.

The *Proceedings of the Biological Society of Washington* (USPS 404-750) is issued quarterly. Back issues of the *Proceedings* and the *Bulletin of the Biological Society of Washington* (issued sporadically) are available. Correspondence dealing with membership and subscriptions should be sent to The Treasurer, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Manuscripts, corrected proofs, editorial questions should be sent to the Editor, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Known office of publication: National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Printed for the Society by Allen Press, Inc., Lawrence, Kansas 66044

Second class postage paid at Washington, D.C., and additional mailing office.

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, National Museum of Natural History, Washington, D.C. 20560.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 209–228

NEW RECORDS OF STYLASTERIDAE (HYDROZOA: HYDROIDA) FROM THE GALÁPAGOS AND COCOS ISLANDS

Stephen D. Cairns

Abstract.—Based on the collections of the *Johnson-Sea-Link I* submersible, new records of 14 stylasterid species are reported from the Galápagos Islands, including one new species: *Lepidopora concatenata.* Five stylasterid species are reported from Cocos Island, including two new species: *Pliobothrus fistulosus* and *Stylaster cocosensis.* These are the first records of stylasterids from Cocos Island, three of the five species also shared with the Galápagos Islands. These specimens are also the first records of the genera *Lepidopora* and *Pliobothrus* in the eastern Pacific, from the Galápagos and Cocos Islands, respectively. Both the Galápagan and Cocos Island stylasterid faunae are considered to be derived from the western Pacific, having no affinity with the shelf and slope fauna of the American continents in the eastern Pacific.

A rich fauna of fourteen stylasterid species, all endemic to the Galápagos Islands and all based on only six *Albatross* stations made at the turn of the century, was reviewed by Cairns (1986b). Therefore, it was anticipated that a more intensive collecting effort (27 stations in the Galápagos and 8 off Cocos Island) using more efficient and selective collecting methods (a manned submersible) would certainly yield many more species. Although stylasterids were sighted on every submersible dive and collected at 21 of the 27 sites in the Galápagos, in which all 14 previously collected species were represented, only one specimen of one new species was collected. This surprising result might be explained by assuming that all of the Galápagan stylasterid species are uniformly and abundantly distributed throughout the archipelago, such that even a cursory sampling would have a high probability of collecting most of the resident species. This hypothesis would explain both the paucity of new species and the re-collection of all previously known species.

The history of our knowledge of the Galápagos stylasterid fauna was given by Cairns (1986b) and is not repeated here. One of the species previously reported, *Stenohelia robusta* Boschma, 1964a, is herein synonymized with *Stenohelia concinna* Boschma, 1964a, and one new species is described, which maintains the number of species known from the Galápagos at 14. The additional specimens collected by the *Johnson-Sea-Link I,* however, did: allow an extension of the geographic, bathymetric, and temperature ranges of all species; provide information on the range of variation of various morphological characters; and establish maximum colony sizes for half of the species.

Stylasterids were also abundant off Cocos Island, being collected from four of the eight stations. Since no stylasterids had previously been reported from Cocos Island, the five species reported herein are all new records for this island, including two new species.

Material and methods.—The new records on which this report is based originated primarily from collections of the *R/V Seward Johnson* and *Johnson-Sea-Link I* submersible expedition to the Galápagos and Cocos

Table 1.—List of *Johnson-Sea-Link I* (*JSL*) stations at which stylasterids were collected (Fig. 32).

Station	Latitude	Longitude (°W)	Depth (m)	Date	Bottom temperature (°C)
1911	0°32.7′S	90°07.0′	426–462	12 Nov 1986	8.3–10.3
1912	0°21.9′S	90°15.7′	713–806	14 Nov 1986	5.9–6.7
1913	1°32.7′S	90°25.8′	84–227	14 Nov 1986	13.5–14.5
1914	1°17.3′S	90°17.4′	166–172	15 Nov 1986	14.3–14.4
1915	1°17.2′S	89°48.7′	650–652	15 Nov 1986	7.4–10.8
1916	1°18.7′S	89°48.8′	545–562	16 Nov 1986	7.3–10.8
1920	1°46.6′S	89°30.8′	64–104	17 Nov 1986	
1921	0°17.0′N	89°59.8′	680–720	18 Nov 1986	6.0–6.7
1922	0°23.7′N	90°26.3′	475–578	19 Nov 1986	7.3–8.9
1923	0°23.7′N	90°32.3′	348–384	19 Nov 1986	9.9–10.0
1924	0°03.9′N	90°19.2′	373–430	20 Nov 1986	
1925	0°14.9′S	90°32.5′	415–447	20 Nov 1986	8.9–9.3
1927	0°10.5′S	90°53.3′	708–784	21 Nov 1986	5.6–6.5
1928	0°15.2′S	91°06.9′	720–813	22 Nov 1986	5.0–7.5
1929	0°14.7′N	91°36.5′	806	23 Nov 1986	5.7–9.3
1931	0°10.3′S	91°24.7′	441–525	24 Nov 1986	7.9–8.0
1932	0°15.1′S	91°27.7′	313–315	24 Nov 1986	10.4–12.2
1933	0°17.1′S	91°40.2′	663–788	25 Nov 1986	6.0–7.0
1935	0°15.2′S	91°27.9′	252–308	25 Nov 1986	7.8–9.0
1936	0°40.7′S	91°24.0′	182–224	26 Nov 1986	12.5–14.4
1937	0°59.8′S	91°27.1′	315–316	27 Nov 1986	11.2–12.6
1940	5°34.6′N	87°04.3′	546–631	1 Dec 1986	9.0
1942	5°34.6′N	87°04.3′	606–628	2 Dec 1986	6.7–7.1
1943	5°26.1′N	87°08.0′	303–333	2 Dec 1986	11.9
1944	5°28.1′N	87°08.0′	293–576	3 Dec 1986	7.7–8.3

Islands in November and December of 1986. Stylasterids were collected at 25 of the 35 submersible sites (Table 1). The use of a manned research submersible allowed selective collection of deep-water invertebrates and in situ observation and photography of living coral, and is highly recommended for the collection of deep-water benthic invertebrates in areas of rugged topography.

Definitions of the terms used in the descriptions are reviewed and illustrated by Cairns (1983b, 1986a). Synonymies are not always complete; where they are not, they include a reference to a complete synonymy. All type and most nontype specimens are deposited at the USNM; a synoptic collection is also deposited at the Charles Darwin Research Station. The scanning electron photomicrographs were done by the author on a Cambridge Stereo Scan 100.

The following abbreviations are used in the text:

CDRS	Charles Darwin Research Station, Santa Cruz, Galápagos
H:W	Height-to-width ratio of a gastrostyle
JSL	*Johnson-Sea-Link I*, a 4-man research submersible owned by the Harbor Branch Oceanographic Institution, Inc., Fort Pierce, Florida
USNM	Collections of the United States National Museum (now housed at the National Museum of Natural History), Smithsonian Institution, Washington, D.C.

Zoogeography.—Cairns (1986b) reported that all 14 stylasterid species known from the Galápagos were endemic. Furthermore, he stated that, at the generic level, the affinities of the Galápagos stylasterids were

with the western Pacific and less so with the western Atlantic, not at all with the eastern Pacific. The deep-water Equatorial Undercurrent was suggested as a possible dispersal mechanism for larvae. The collections of the *Johnson-Sea-Link I* expedition reinforce this interpretation. At the species level, three Galápagan species are now known from Cocos Island and one, *Crypthelia cymas,* is known from off New Zealand (Cairns 1991c). This observation, along with the discovery of *Lepidopora* in the Galápagos (a widespread genus but not known elsewhere in the eastern Pacific) reinforces the hypothesis of a western Pacific origin of the Galápagan stylasterid fauna.

Five stylasterid species are known from off Cocos Island, belonging to three genera: *Pliobothrus fistulosus, Errina macrogastra, Stylaster marenzelleri, S. galapagensis,* and *S. cocosensis.* At the species level, two of the five are known only from Cocos Island, the remaining three also occurring in the Galápagos Islands. All three genera have widespread distributions but do not occur in the eastern Pacific. Thus, although based on relatively few specimens, it would appear that the Cocos Island fauna is also primarily influenced from the western, not eastern, Pacific. This is contrary to the indication of Briggs (1974), based on shallow-water invertebrates and shore fish, and Cairns (1991a), based on ahermatypic Scleractinia, who both considered Cocos Island as an extension of the Panamanian Province. But it must be remembered that the Cocos stylasterid fauna is a predominantly deep water one (e.g., 300–800 m) and therefore probably not influenced by the shallow water currents from the Panamanian mainland.

New Records

Family Stylasteridae Gray, 1847

Lepidopora concatenata, new species

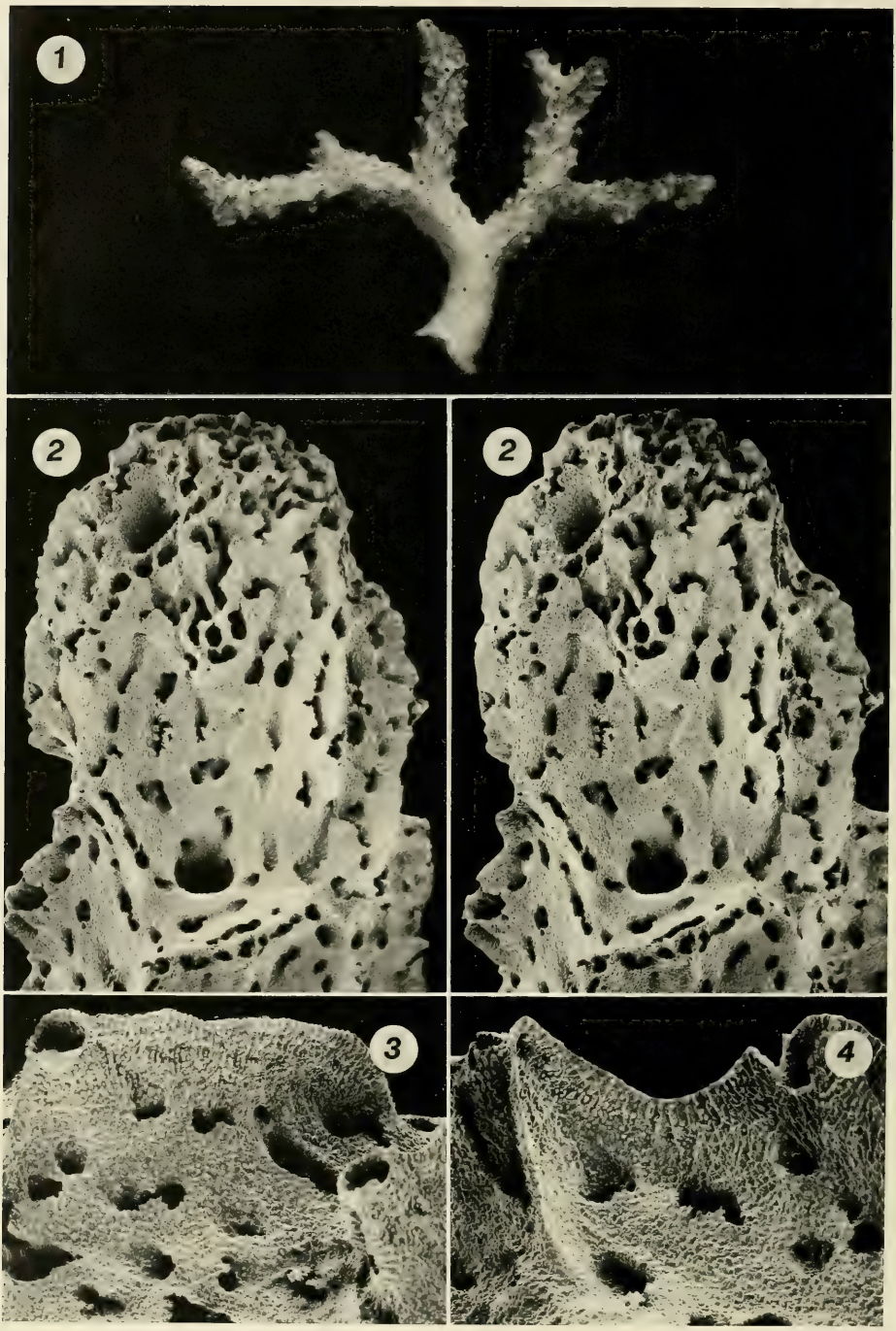
Figs. 1–7

Records.—Holotype: *JSL*-1921, 0°17'N, 89°59.8'W (southwest of Genovesa, Galápagos Islands), 680–720 m, 1 colony and SEM stub 698, USNM 84697.

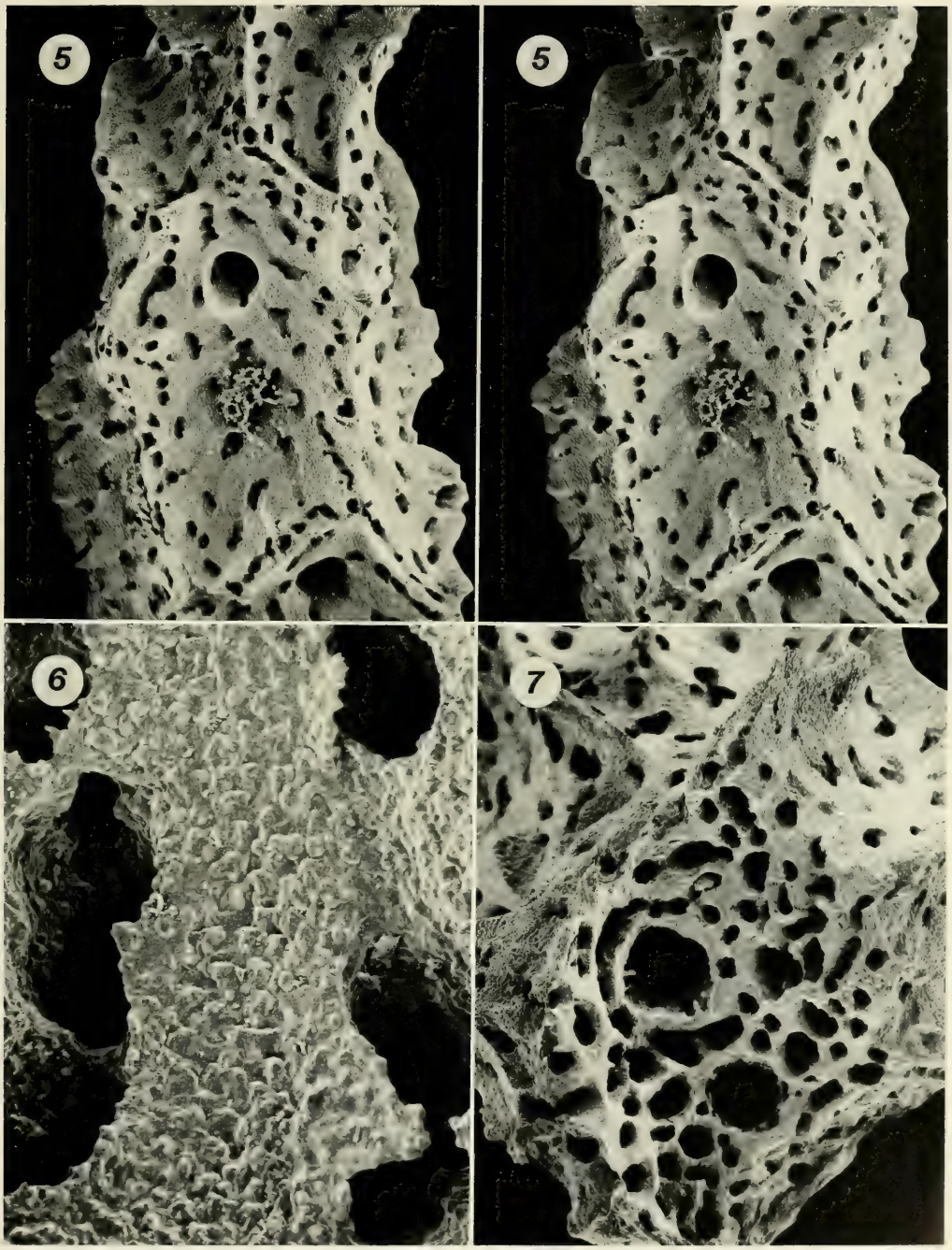
Description.—Colony uniplanar and relatively small, the holotype 20.4 mm tall and 30.2 mm broad, with a basal branch diameter of 3.2 mm. Branching sparse, dichotomous, and equal, resulting in a fairly symmetrical branching pattern. Branches circular in cross section, terminating in tips about 1.8 mm in diameter; no branch anastomosis. Coenosteum white and reticulate-imbricate in texture. Coenosteal strips broad but variable in width, ranging from 0.11 to 0.20 mm across and separated by a series of quite broad (about 66 μ wide), elliptical to elongate coenosteal pores and shallow grooves. Platelet structure poorly defined (Fig. 6), the platelets being only 18–35 μ wide.

Gastropores uniformly distributed on branch surfaces, circular in shape (0.31–0.33 mm in diameter), and flush with coenosteal surface (no gastropore lips). Gastropore tubes cylindrical and deep, each bearing a diffuse ring palisade composed of blunt, cylindrical elements up to 45 μ tall and 17 μ in diameter. Because only one specimen was available for study, a fragment was not sacrificed to examine and figure a gastrostyle; however, from gross external examination, gastrostyles appear to be elongate and slender, probably with a relatively high H:W ratio. Dactylopores arranged along sinuous, longitudinal or oblique ridges that occasionally anastomose into a reticulate pattern (Figs. 2, 5). Dactylopores circular to elliptical in shape: circular dactylopores about 85 μ in diameter, elliptical ones up to 118 μ in greater diameter. Ridges on which dactylopores occur quite tall (up to 0.5 mm) and thin (25–30 μ wide), dactylopore centers spaced every 0.5–0.8 mm along ridge. Dactylopores are the most prominent sections of a ridge, the ridge connecting adjacent pores sometimes slightly lower in height.

Colony sexually immature and therefore sex and characteristics of ampullae unknown.



Figs. 1–4. *Lepidopora concatenata,* holotype, USNM 84697: 1, Holotype colony, ×2.3; 2, Branch tip illustrating tall dactylopore ridges and one gastropore, ×25.5, stereo pair; 3, 4, Elongate ridges concatenating (linking) dactylopores, ×56, ×62, respectively.



Figs. 5–7. *Lepidopora concatenata,* holotype, USNM 84697: 5, Branch segment illustrating two gastropores and ridges linking dactylopores, ×21, stereo pair; 6, Weakly imbricate coenosteal texture, ×180; 7, Branch cross section revealing porous central core, two gastropores in cross section, and tall coenosteal ridges peripherally, ×38.

Discussion.—Among the 25 valid species of *Lepidopora* (see Cairns 1991c), *L. concatenata* is most similar to *L. acrolophos* Cairns, 1983a, known only from the Scotia Ridge west of South Georgia (659–686 m). Both species have: similarly sized and shaped coralla and branching pattern; linked dactylopores; same sized gastro- and dactylopores; and the same bathymetric range. *Lepidopora acrolophos,* however, differs in having a very different coenosteal texture (reticulate-papillose), small abcauline gastropore lips, dactylopores that are sometimes not linked by ridges, and in lacking ring palisades.

Although less similar to *L. concatenata, L. polystichopora* Cairns, 1985 (north of New Zealand, 197–710 m) also sometimes has linked dactylopores as well as having equal branching and primarily imbricate coenosteal texture. But *L. polystichopora* differs in having its dactylopores arranged in four to seven discrete, longitudinal rows, the ridges uniting the dactylopores being quite low (about 0.12 mm); having small, abcauline gastropore lips; and in lacking ring palisades.

In addition to *L. concatenata,* only one other species of *Lepidopora* has ring palisades: *L. glabra* (Pourtalès, 1867), known only from the Straits of Florida at 267–1170 m (see Cairns 1986a). *L. glabra,* however, shares few other characters, differing in: coenosteal texture; arrangement of gastro- and dactylopores; having unlinked dactylopores; and in having quite large abcauline gastropore lips. The character of tall, slender ridges that consistently link its dactylopores is unique to *L. concatenata.*

Etymology.—The species name *concatenata* (Latin for "linked together") refers to the dactylopores of this species, which are linked together by tall, thin ridges.

Distribution.—Species known only from type locality. *Lepidopora* is a wide ranging genus known from throughout the Atlantic, Subantarctic, and South Pacific (New Zealand region) from depths of 60–1874 m (Cairns 1991b); thus, this is the first record of the genus for the eastern Pacific.

Pliobothrus fistulosus, new species
Figs. 8–14

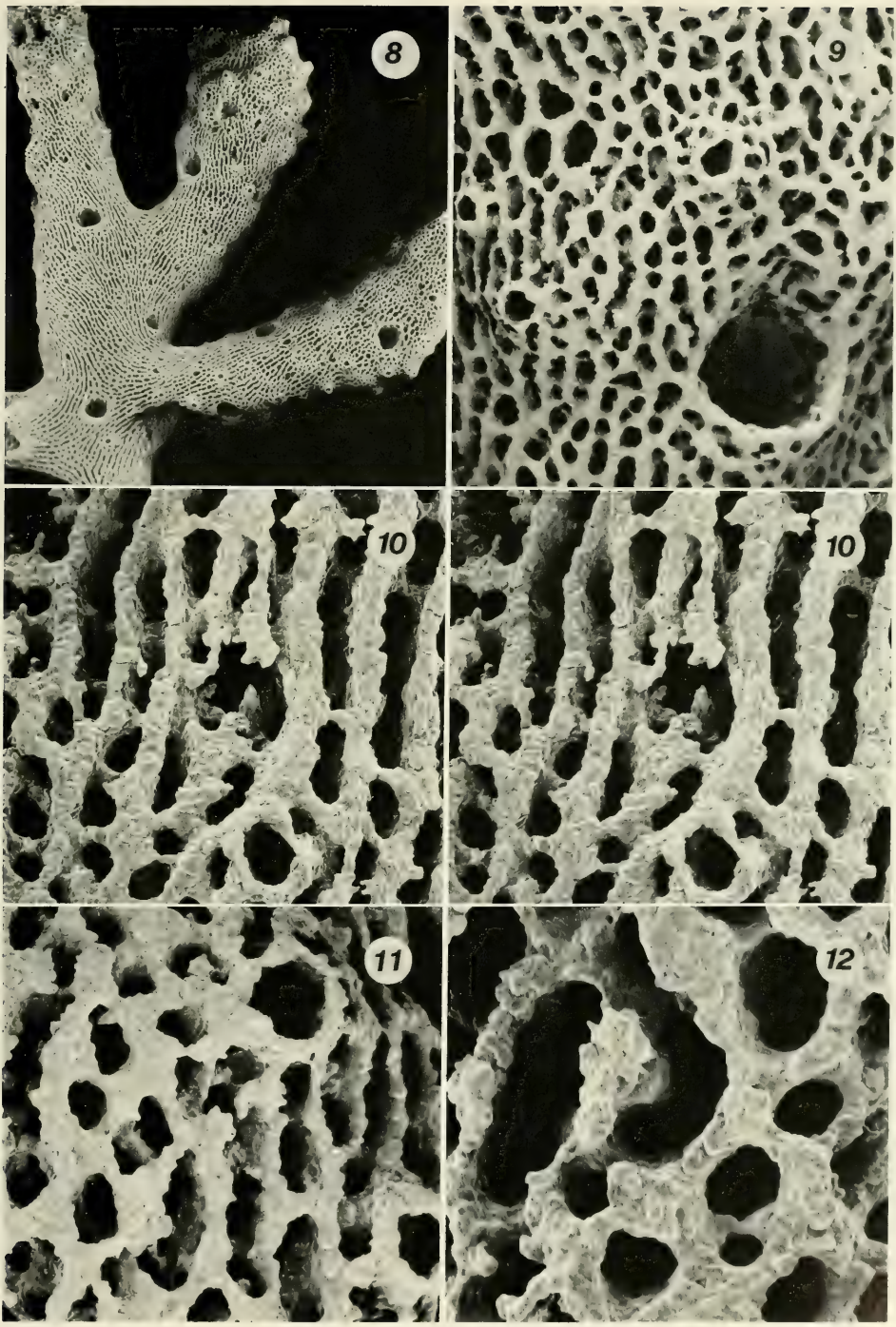
Records.—Holotype: *JSL*-1940, 5°34.6′N, 87°04.2′W (north coast of Cocos Island), 546–631 m, 9°C, 1 colony (ex SEM stub 699), USNM 84696.

Description.—Colony probably uniplanar, the only known specimen (the holotype) a colony fragment 11.0 mm tall and 10.5 mm broad, consisting of 3 terminal branches. Branching dichotomous and apparently equal; branches circular to slightly elliptical in cross section, having blunt to slightly clavate tips 1.8–2.2 mm in diameter. Coenosteum white and linear-imbricate in texture. Coenosteal strips quite thin (21–45 μ wide), bordered by deep, elongate slits that are often equal to or wider than strip width (e.g., up to 55 μ wide). Slits traversed by narrow (20–23 μ wide) coenosteal bridges (Fig. 10). Platelets very poorly defined but present in a unilinear series on each strip.

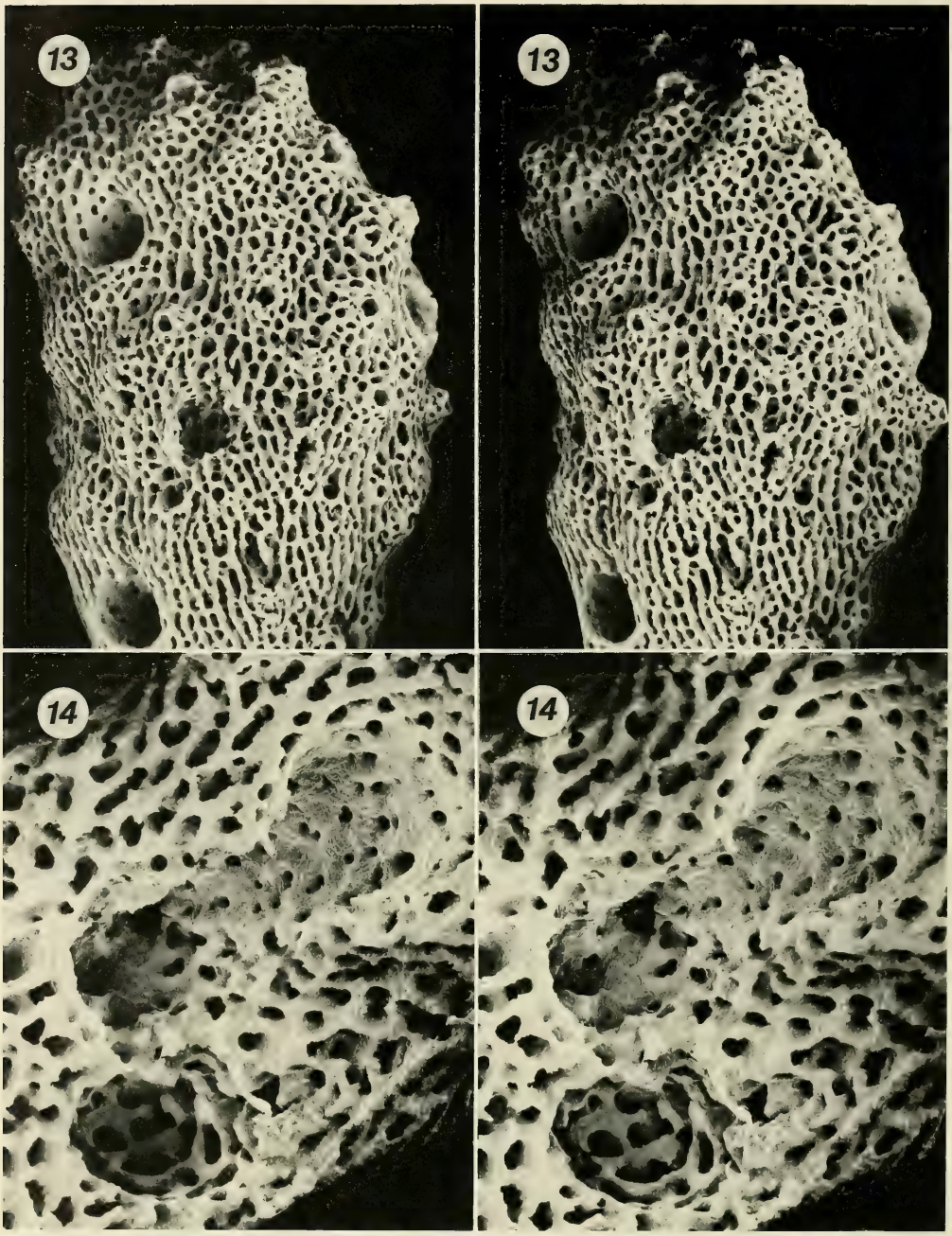
Gastropores uniformly distributed on all branch surfaces, circular in shape (0.37–0.39 mm in diameter), and flush with coenosteal surface. Gastropore tubes cylindrical with a slightly enlarged lower section, and bent about 90°, the lower section running parallel to branch axis. Total length of gastropore tube 0.9–1.0 mm. No ring palisades or tabulae present. Dactylopores also uniformly distributed on branch surfaces and circular in shape: 86–93 μ in diameter. Dactylopores elevated on cylindrical mounds as high as 0.2 mm, the thin walls of the mound 15–20 μ thick, resulting in a dactylopore mound diameter of 0.12–0.13 mm.

Sex of holotype probably female. Ampullae internal, 0.3–0.4 mm in diameter, and communicate to coenosteal surface through an inconspicuous, spongy efferent pore about 0.10 mm in diameter.

Discussion.—Four Recent species of *Pliobothrus* are known: *P. tubulatus* (Pour-



Figs. 8–12. *Pliobothrus fistulosus,* holotype, USNM 84696: 8, Holotype colony, ×7.0; 9, Branch segment illustrating one gastropore and two smaller dactylopores, ×44; 10, Porous coenosteal texture with irregularly-shaped efferent pore in center, ×92, stereo pair; 11, Porous coenosteal texture (dactylopore in upper right), ×110; 12, Enlargement of coenosteal texture, ×170.



Figs. 13, 14. *Pliobothrus fistulosus,* holotype, USNM 84696: 13, Branch tip bearing a concave, ruptured ampulla (left center), ×20.5, stereo pair; 14, Longitudinal section of a gastropore tube (above) and internal ampulla (below), ×46, stereo pair.

talès, 1867) (Antilles, 419–718 m); *P. symmetricus* Pourtalès, 1868 (North Atlantic, 80–1600 m); *P. spinosus* (Hickson & England, 1905) (Indonesia, 1089 m); and *P. echinatus* Cairns, 1986a (Lesser Antilles, 164–708 m). *Pliobothrus fistulosus* differs from all of these species in having extremely narrow coenosteal strips and much smaller ampullae. Its dactylopore mounds are about the same height as those of *P. symmetricus* (0.2 mm), but considerably shorter than those of *P. spinosus* (1.2 mm), *P. tubulatus* (0.8 mm), and *P. echinatus* (0.4 mm). It is further differentiated from *P. symmetricus* by having less robust branches.

Etymology.—The species name *fistulosus* (Latin for "forming a pipe," "hollow," or "porous") could be interpreted in any of three ways: forming a pipe, alluding to its long axial gastro- and dactylopores, which give the branch a very porous cross section; hollow, referring to the numerous axial gastro- and dactylopores and the numerous rather large coenosteal pores that penetrate the coenosteum; and "porous," as a general designation for the highly permeable nature of the coenosteum.

Distribution.—Known only from the type locality. Species of *Pliobothrus* are known from the North Atlantic and Indonesian region from depths of 80–1600 m (Cairns 1991b); therefore, this is the first record of the genus from the eastern Pacific.

Lepidotheca macropora Cairns, 1986
Fig. 15

Lepidotheca macropora Cairns, 1986b:4–6, figs. 1A–G, 2A–C.

New records.—*JSL* Stations 1914, 16 colonies, USNM 84698; 1924, 3 colonies, USNM 84699; 1929, 5 colonies and branches, USNM 84700; 1932, 3 colonies and branches, USNM 84701; 1933, 1 branch, USNM 84702; 1937, 1 colony, USNM 84703.

Discussion.—Previously known from only two localities in the Galápagos, 29 additional colonies of *L. macropora* are herein reported from six more localities, extending its range into the western islands of the Galápagos. Considerably larger specimens were collected during the *JSL* expedition, the largest (*JSL*-1914) a uniplanar colony 7.7 cm tall and 9.1 cm broad, with a basal branch diameter of 7.5 mm (Fig. 15). The tissue is a characteristic light brown; the corallum is white. Branches are elliptical to flattened in cross section; the distal, small-diameter branches being flattened in the plane of the colony. Although abcauline dactylopore spines are clearly present on most branches, dactylopore spines are often quite small and low, and have very short, obscure dactylotomes, thus sometimes superficially resembling species of *Lepidopora*.

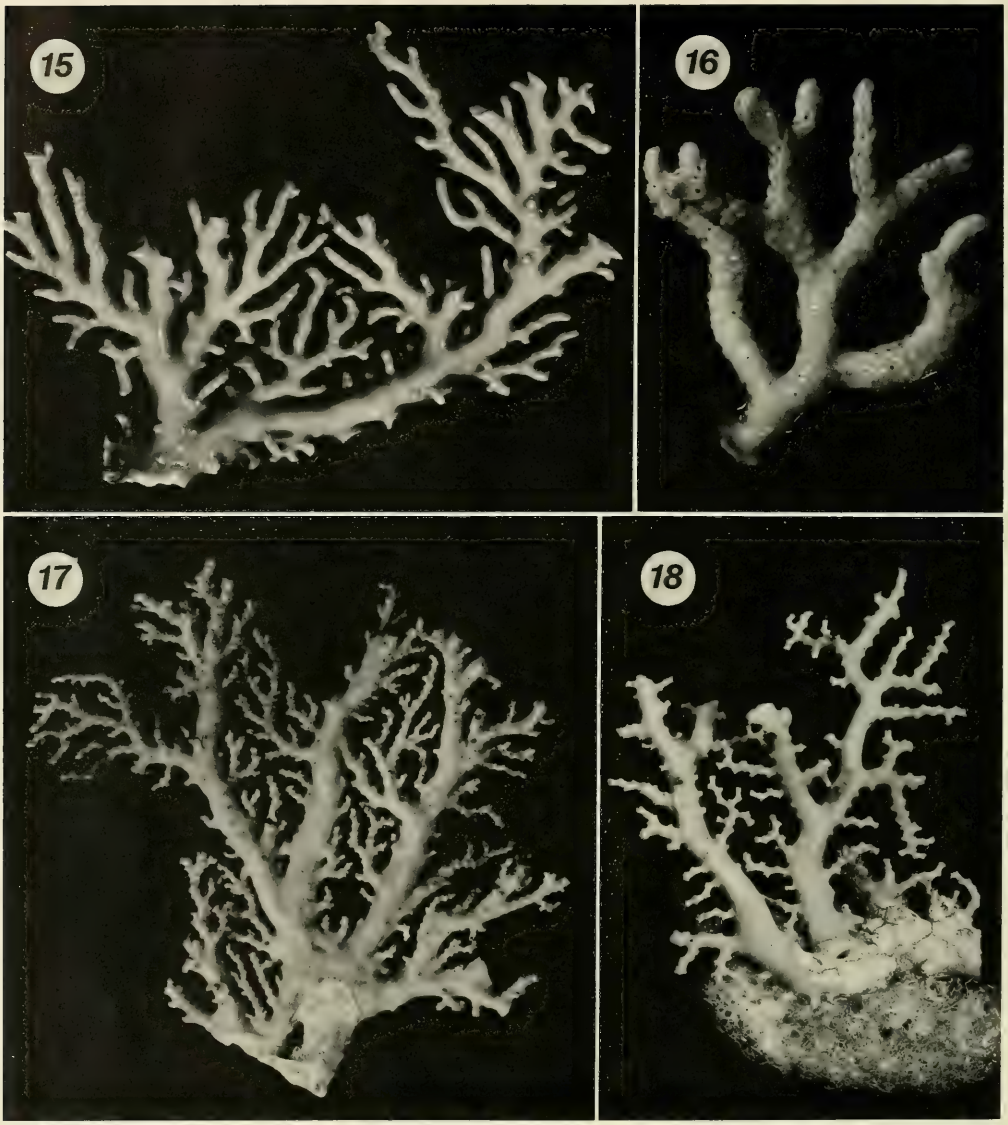
Distribution.—Widespread throughout Galápagos, including off: Fernandina, Isabela, south of Marchena, northeast of Santa Cruz, Española, and Floreana; 166–806 m; 5.7°–14.4°C.

Distichopora laevigranulosa Cairns, 1986
Fig. 16

Distichopora laevigranulosa Cairns, 1986b: 6–8, figs. 3A–I.

New records.—*JSL* Stations 1911, 1 female colony, USNM 84704; 1914, 2 female colonies, USNM 84705; 1916, 1 female colony, USNM 84706; 1929, 2 female colonies, USNM 84707.

Discussion.—*Distichopora laevigranulosa* was previously known from only one branch fragment (the holotype); six additional specimens from four more localities are recorded herein. The largest, and complete, colony is 31.0 mm tall and 3.95 mm broad, with a basal branch diameter of 5.2 × 6.2 mm (*JSL*-1929). It has equal, sparse branching, resulting in only 10 branch tips (Fig. 16). Tissue light brown; corallum white. The holotype has several gastropores on its anterior face; however, the colony from *JSL*-1916 has numerous gastropores on its anterior face in addition to those constituting the lateral edge pore row. Another point of



Figs. 15–18. 15, *Lepidotheca macropora, JSL*-1914, USNM 84698, ×0.81; 16, *Distichopora laevigranulosa, JSL*-1929, USNM 84707, female colony, ×1.2; 17, *Stylaster marenzelleri, JSL*-1923, USNM 84730, male colony, ×0.8; 18, *Stylaster cocosensis,* holotype, USNM 84734, ×1.3.

variation is that one of the dactylopore rows of the specimen from *JSL*-1911 has almost completely degenerated, the opposite row appearing to be the only functional dactylopores. The holotype, as well as all six specimens reported here, are mature female colonies, thus male ampullae remain unknown.

Distribution.—Off Roca Redonda, Santa Cruz, Española, and Floreana; 166–806 m; 5.7°–14.4°C. Species of *Distichopora* are common in the Indo-West Pacific (Boschma 1959) and western Atlantic (Cairns 1983a), but are conspicuously absent from the Antarctic-Subantarctic region and eastern Atlantic. *Distichopora laevigranulosa* is

the only record of the genus from the eastern Pacific.

Errina macrogastra Marenzeller, 1904

Errina macrogastra Marenzeller, 1904:81–83, pl. 2, fig. 1, pl. 3, fig. 1.—Cairns, 1986b: 8–9, figs. 4A–G, 5A–C (synonymy).

New records.—*JSL* Stations 1916, 2 female, 4 male, and 1 immature colonies, USNM 84708; 1942, 1 male and 1 immature colonies, USNM 84709.

Discussion.—Previously known from between Española and San Cristóbal (Cairns 1986b), *E. macrogastra* is herein reported from two additional stations: one also from near Española, the other north of Cocos Island. The Galápagan specimen is typical of previously collected specimens, but the Cocos Island specimens are more delicate in construction, having elongate, slender branch tips as small as 0.5 mm in diameter.

Distribution.—Off San Cristóbal and Española, Galápagos; north of Cocos Island; 545–704 m; 6.2°–10.8°C.

Stylaster divergens Marenzeller, 1904

Stylaster divergens Marenzeller, 1904:83–86, pl. 2, fig. 3, pl. 3, fig. 2.—Cairns, 1986b: 11–14, figs. 6A–G, 7A–C (synonymy).

New records.—*JSL* Stations 1914, 4 colonies, USNM 84721; 1920, 4 colonies, USNM 84722; 1936, 1 female colony, USNM 84723; off Daphne Minor, 55 m, coll. Hydes and Summerhays, June 1974, 1 male colony, USNM 84724.

Discussion.—Colonies from four additional Galápagos localities are reported herein, including one large specimen 7 cm tall (*JSL*-1914). Although most colonies have a white corallum, several from *JSL*-1920 have a rich purple-violet corallum, both white and pigmented corolla co-occurring. A bright red foraminiferan is often found encrusting the base of colonies, *S. divergens* being the shallowest occurring stylasterid in the Galápagos.

Distribution.—Off southwestern Isabela, Daphne Minor, San Cristóbal, and Floreana; 55–224 m; 12.5°–23.4°C.

Stylaster marenzelleri Cairns, 1986
Fig. 17

Stylaster marenzelleri Cairns, 1986b:14–16, figs. 8A–F, 9A, B.

New records.—*JSL* Stations 1911, 2 colonies, USNM 84727; 1913, 1 branch, USNM 84728; 1914, 6 branches, USNM 84729; 1923, 4 colonies, USNM 84730; 1924, 7 colonies, USNM 84731; 1937, 2 colonies, USNM 84732; 1940, 1 branch, USNM 84733.

Discussion.—Previously known from only the type locality off Española, *S. marenzelleri* is herein reported from seven additional localities, including off Cocos Island. Several large specimens were collected, one (*JSL*-1923) 7.8 cm tall and 8.7 cm broad, with a basal branch diameter 6.5 mm in lesser diameter (Fig. 17). Some branch anastomosis occurs in this specimen. All coralla are light pink; however, some have white branch tips and basal encrustations. All medium- to large-sized specimens live in association with a eunicid polychaete, which live in tubes 0.6–0.8 mm in diameter along the axis of larger branches. In some branches, two closely adjacent tubes are present. The tube penetrates the coenosteal surface periodically near the branch tips. *S. marenzelleri* is the only Galápagos stylasterid to have axial polychaete tubes; however, *S. cocosensis* from Cocos Island has a similar commensalism.

Distribution.—Known from throughout the Galápagos, including off: Isabela, Marchena, Santa Cruz, Española, and Floreana; north of Cocos Island; 84–631 m; 8.3°–14.5°C.

Stylaster galapagensis Cairns, 1986

Stylaster galapagensis Cairns, 1986b:16–18, figs. 10A–H, 11A–C.

New records.—*JSL* Stations 1911, 4 colonies, USNM 84710; 1921, 2 colonies, USNM 84711; 1922, 2 colonies, USNM 84712; 1924, 9 colonies, USNM 84713; 1925, 4 branches, USNM 84714; 1927, 1 colony, USNM 84715; 1929, 14 colonies, USNM 84716; 1931, 2 colonies, USNM 84717; 1935, 1 colony, USNM 84718; 1938, 5 colonies, USNM 84719; 1944, 2 colonies, USNM 84720.

Distribution.—Previously known from only two stations in the western Galápagos Islands, 11 additional records of *S. galapagensis* are reported herein, showing it to be widespread throughout the Galápagos, as well as off Cocos Island, including: off Fernandina, Isabela, Roca Redonda, Marchena, Genovesa, Española, Santa Cruz, and Santiago; 252–806 m; 5.8°–10.3°C.

Stylaster cocosensis, new species
Figs. 18–25

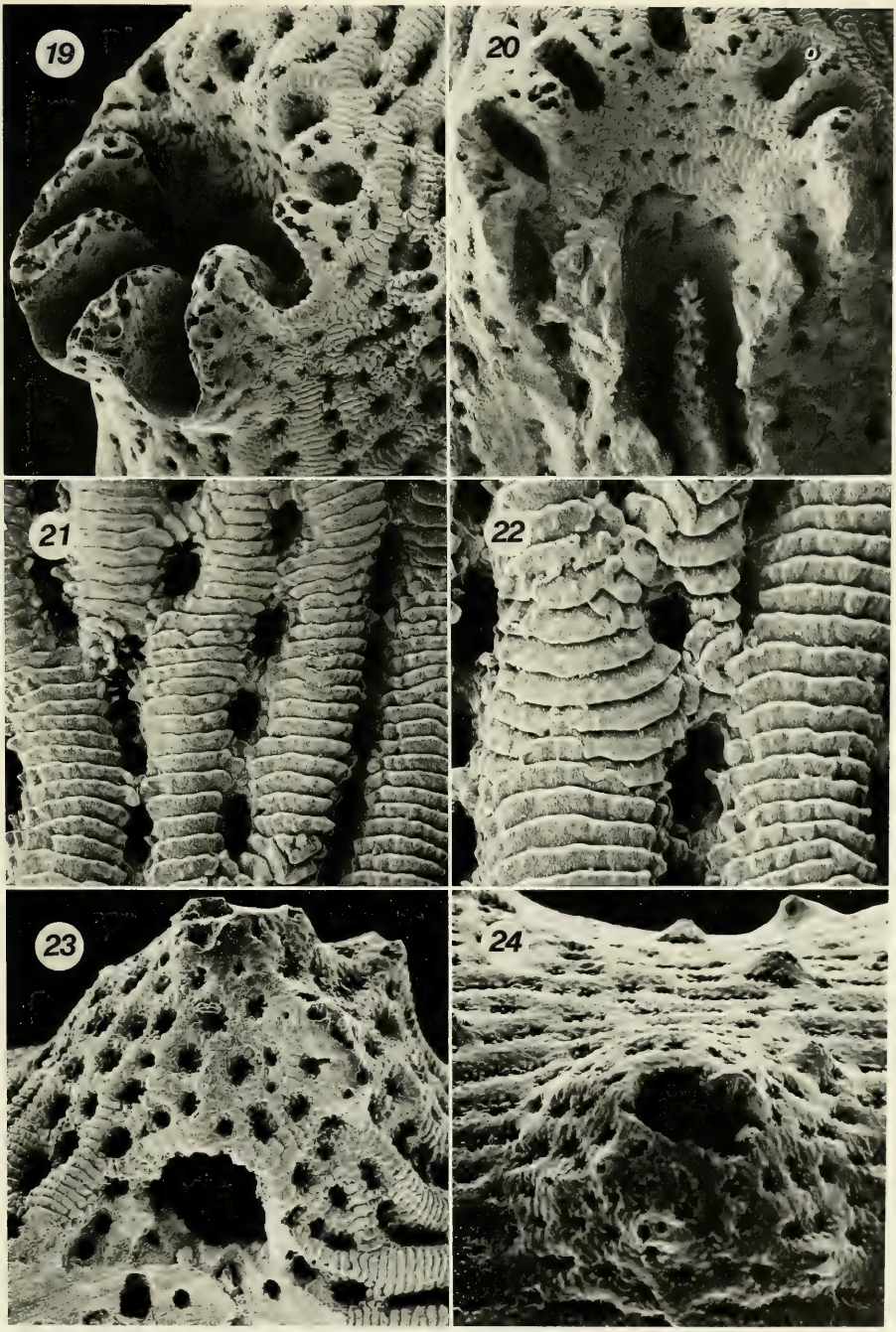
Records.—Holotype: *JSL*-1944, 5°28.1'N, 87°08'W (southwest coast of Cocos Island), 293–576 m, 1 male colony and SEM stub 704, USNM 84734.—Paratypes: *JSL* Stations 1943, 2 male colonies and branches, USNM 84735; 1944, 4 female colonies, branches, and SEM stub 703, USNM 84736.

Description.—Colonies uniplanar, the largest colony (holotype) 38.0 mm tall and 32.2 mm broad, with a basal branch diameter of 4.5 mm. Branching dichotomous and unequal, densely branched but lacking branch anastomosis. Branches circular in cross section, the distal branches slender and fragile. Symbiotic polychaetes usually present but do not significantly alter colony shape (see Remarks). Coenosteum white, with well-developed, linear-imbricate coenosteum. Coenosteal strips 40–80 μ wide, separated by relatively wide and deep slits 15–20 μ wide. Slits periodically traversed by thick coenosteal bridges, which reduce the coenosteal slits to a series of elongate, elliptical pores (Figs. 21, 22). Platelets well developed, usually continuous across a strip, and slightly corrugated; alternating platelet polarity not unusual (Fig. 22). Older or worn coenosteum appears to be linear-granular or linear-smooth in texture, the imbricate platelets being worn or secondarily covered. Nematopores uniformly and abundantly distributed on branch coenosteum. Basal diameter of nematopore mounds 50–70 μ, apical pit 13–16 μ in diameter, and height of mounds up to 15 μ.

Cyclosystems exclusively sympodially arranged on branch edges. Cyclosystems small (0.4–0.6 mm in diameter) and circular to slightly elliptical in shape. Based on 50 cyclosystems, the range of dactylopores per cyclosystem was 5–12, average 8.41 (σ = 1.45), and mode 9.

Gastropore tubes consist of two sections: a broad, upper, chaliciform section about 0.35 mm in diameter and 0.3–0.4 mm deep, and a lower, cylindrical section about half this diameter and about 0.5 mm deep, which the gastrostyle occupies. Ring palisades absent. Upper section linear-imbricate in texture, 3 or 4 coenosteal strips encircling the tube; lower tube porous, not textured. Gastrostyle elongate-conical to needle-shaped: illustrated style (Fig. 20) 0.39 mm tall and 50 μ in diameter (H:W ratio 7.2), its tip rising almost to junction between upper and lower gastropore sections. Upper three-quarters of gastrostyle covered with smooth, sharp spines up to 20 μ long. Dactylotomes 55–75 μ wide but extend only a short distance down gastropore tube. Pseudosepta wedge-shaped, about 0.13 mm wide at their outer edges, and consistently well developed on terminal cyclosystems. Cyclosystems on older branches, however, often develop diastemas of variable width by the atrophy of adcauline (distal) dactylopores. Dactylostyles consist of a unilinear row of small, cylindrical elements.

Female ampullae (Fig. 23) prominent hemispheres 0.35–0.45 mm in diameter, occurring on anterior and posterior branch faces. Coenosteum of female ampullae porous, each ampulla bearing 5–8 short, apical



Figs. 19–24. *Stylaster cocosensis, JSL*-1924, paratypes, USNM 84735: 19, Cyclosystem, ×98; 20, Longitudinal section of a gastropore tube revealing the gastrostyle, ×86; 21, 22, Linear-imbricate coenosteal texture, ×200, ×300, respectively; 23, Female ampulla with efferent pore, ×125; 24, Male ampulla with apical efferent pore, ×110.

(about 50 μ tall) spines. Female efferent pore lateral: 0.10–0.12 mm in diameter. Spent female ampullae often distintegrate, resulting in coenosteal cavities. Male ampullae (Fig. 24) superficial mounds 0.25–0.40 mm in diameter, each with a single apical efferent pore about 40 μ in diameter.

Remarks.—Most specimens examined lived in association with a eunicid polychaete that formed a pair of tubes along the branch axis. The worm tubes are circular in cross section, 0.30–0.57 mm in diameter, and visible only in branch cross section or at infrequent escape pores along the branch coenosteum. Only a thin septum separates one axial tube from the other.

Polychaete commensalism among species of *Stylaster* (Group C) is rare, known only in *S. amphelioides* Kent, 1871 and *S. spatula* Cairns, 1986a, the latter having inconspicuous, internal, axial tubes like those of *S. cocosensis*. *Stylaster marenzelleri* Cairns, 1986b, known from the Galápagos and Cocos Island but a member of *Stylaster* (Group B), also has internal, axial eunicid polychaete tubes that are similar to those of *S. cocosensis*.

Discussion.—Roughly one-third of all stylasterid species belong to the genus *Stylaster* (80/224, Cairns 1991b), and they are badly in need of revision, which makes the description of yet another new species a difficult matter. In order to facilitate comparison, I (Cairns 1983b) divided *Stylaster* into three "groups" (referred to as Groups A–C) of species based primarily on the location of their cyclosystems. *Stylaster cocosensis* falls into Group C, along with 35 other Recent species that have exclusively sympodially arranged cyclosystems and rudimentary dactylostyles. *Stylaster cocosensis* was directly compared to 33 of the 35 species in its group: the types or type fragments of 27 of these species are deposited at the USNM and another six species are represented as nontype specimens. Only specimens of *S. ramosus* Broch, 1947 and *S. microstriatus* Broch, 1936 were lacking. *Stylaster cocosensis* was found to be most similar to *S. duchassaingi* Pourtalès, 1867 (Caribbean, 42–692 m), particularly in: corallum size and shape; coenosteal color and texture; having well-developed nematopores; having papillose female ampullae; and in gastrostyle shape. *S. cocosensis* differs in having smaller cyclosystems, fewer dactylopores per cyclosystem, and in having a polychaete commensal.

Only one other *Stylaster* (Group C) is known from the Galápagos and Cocos Islands, *S. galapagensis* Cairns, 1986b. *Stylaster cocosensis* differs from this species in having linear-imbricate coenosteal texture, smaller cyclosystems, fewer dactylopores per cyclosystem, and porous ampullae. In general, *S. cocosensis* can be distinguished by its linear-imbricate coenosteal texture (although many other species have this texture); small cyclosystems; porous, papillose female ampullae; and inconspicuous polychaete symbiosis.

Etymology.—Named for the island from which it was collected.

Distribution.—Known only from off Cocos Island, 293–576 m.

Stenohelia concinna Boschma, 1964
Figs. 26, 27

Stenohelia concinna Boschma, 1964a:69, 70, pl. 1, figs. 1–6.—Boschma, 1964b:74–77, pls. 1, 2.—Cairns, 1986b:21–24, figs. 14A–G, 15A, B, 27E (synonymy).

Stenohelia robusta Boschma, 1964a:69–72, pl. 1, figs. 7–9.—Cairns, 1986b:19–21, figs. 12A–G, 13A–C, 27A, B, D (synonymy).

New records.—*JSL* Stations 1911, 11 colonies, USNM 84739; 1914, 5 colonies, USNM 84740; 1915, 1 colony, USNM 84741; 1916, 7 colonies, USNM 84742; 1922, 3 colonies, USNM 84743; 1923, 1 colony, USNM 84744; 1924, 12 colonies, USNM 84745; 1927, 1 colony, USNM 84746; 1929, 10 colonies, USNM 84747; 1931, 1 colony, USNM 84748; 1932, 4 colonies, USNM 84749; 1937, 5 colonies,

USNM 84750; *Albatross*-2818, 8 colonies, USNM 52243.

Discussion.—*Stenohelia concinna* and *S. robusta* were previously known only from their type-localities: two *Albatross* stations in the Galápagos. The *Johnson-Sea-Link* expedition provided 70 additional colonies from 13 localities throughout the Galápagos, showing it to be a widespread species and more variable than previously thought. For instance, one large, bushy colony from *JSL*-1929 (Fig. 27) is 14 cm tall and 14 cm broad, with a basal branch diameter of 1.5 cm, which is considerably larger than previously known specimens. Large colonies have numerous, globular, polychaete galls (Fig. 26), one often occurring at each major branch axil. It was also noted that the porosity and size of ampullae is variable within the species, the female ampullae varying from 0.45 to 0.65 mm in diameter and not always as highly porous as those of the type specimens.

Stenohelia robusta was originally (Boschma 1964a) and subsequently (Cairns 1986b) distinguished from *S. concinna* by its more robust branches (thicker axils) and more porous ampullae. Otherwise, the species were considered to be very similar, having the same: coenosteal texture, gastrostyle and gastropore tube shape, ampullar sexual dimorphism, number of dactylopores per cyclosystem, and the same species of polychaete symbiont (Cairns 1986b). All but one of the newly examined 70 specimens pertain to typical *S. concinna,* only one specimen from *JSL*-1915 to *S. robusta,* the latter specimen collected with typical *S. concinna.* As stated above, range of size and porosity of the female ampullae of *S. concinna* is variable, which leaves only the robust growth form to distinguish *S. robusta.* Because of the many other similarities between the two species, *S. robusta* is herein considered as simply the robust growth form of typical *S. concinna.*

Distribution.—Widespread throughout the Galápagos, including off: Fernandina, Isabela, Roca Redonda, Marchena, Santiago, Santa Cruz, San Cristóbal, Española, and Floreana; 166–806 m; 5.6°–14.4°C.

Crypthelia eueides Cairns, 1986
Figs. 28, 29

Crypthelia eueides Cairns, 1986b:25–27, figs. 16A–J, 17A–C, 27F, I.

New records.—*JSL* Stations 1922, 1 male colony, USNM 84758; 1928, 2 female colonies, USNM 84759.

Discussion.—The only variation noted in the *JSL* specimens was that each male ampulla of the colony from *JSL*-1921 has a porous apical projection up to 0.3 mm tall and 0.2 mm in diameter (Figs. 28, 29). These circumferential, spiniform processes result in a coarse appearance of the cyclosystems and corallum.

Distribution.—Off eastern Isabela, Marchena, and southeast of Santa Cruz; 475–813 m; 5.0°–8.9°C.

Crypthelia glebulenta Cairns, 1986
Figs. 30, 31

Crypthelia glebulenta Cairns, 1986b:27–29, figs. 18A–H, 19A, B.

New records.—*JSL* Stations 1914, 7 female colonies, USNM 84762; 1929, 8 male colonies, USNM 84763; 1937, 2 female colonies, USNM 84764.

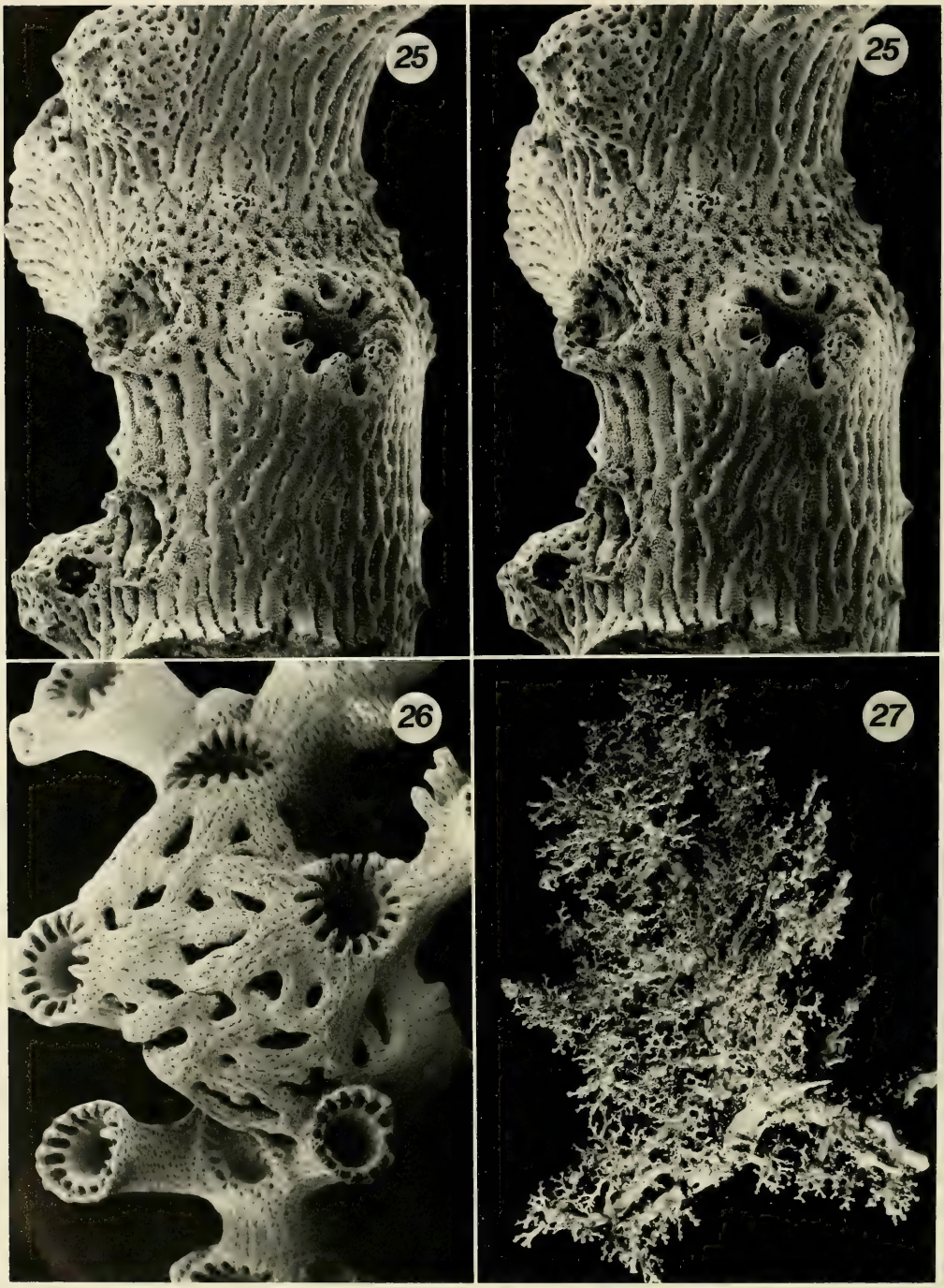
Distribution.—Previously known only from the type locality off Santa Cruz, three more localities are reported herein, from: off southwestern Isabela, Roca Redonda, and Floreana; 166–806 m; 5.7°–14.4°C.

Crypthelia lacunosa Cairns, 1986

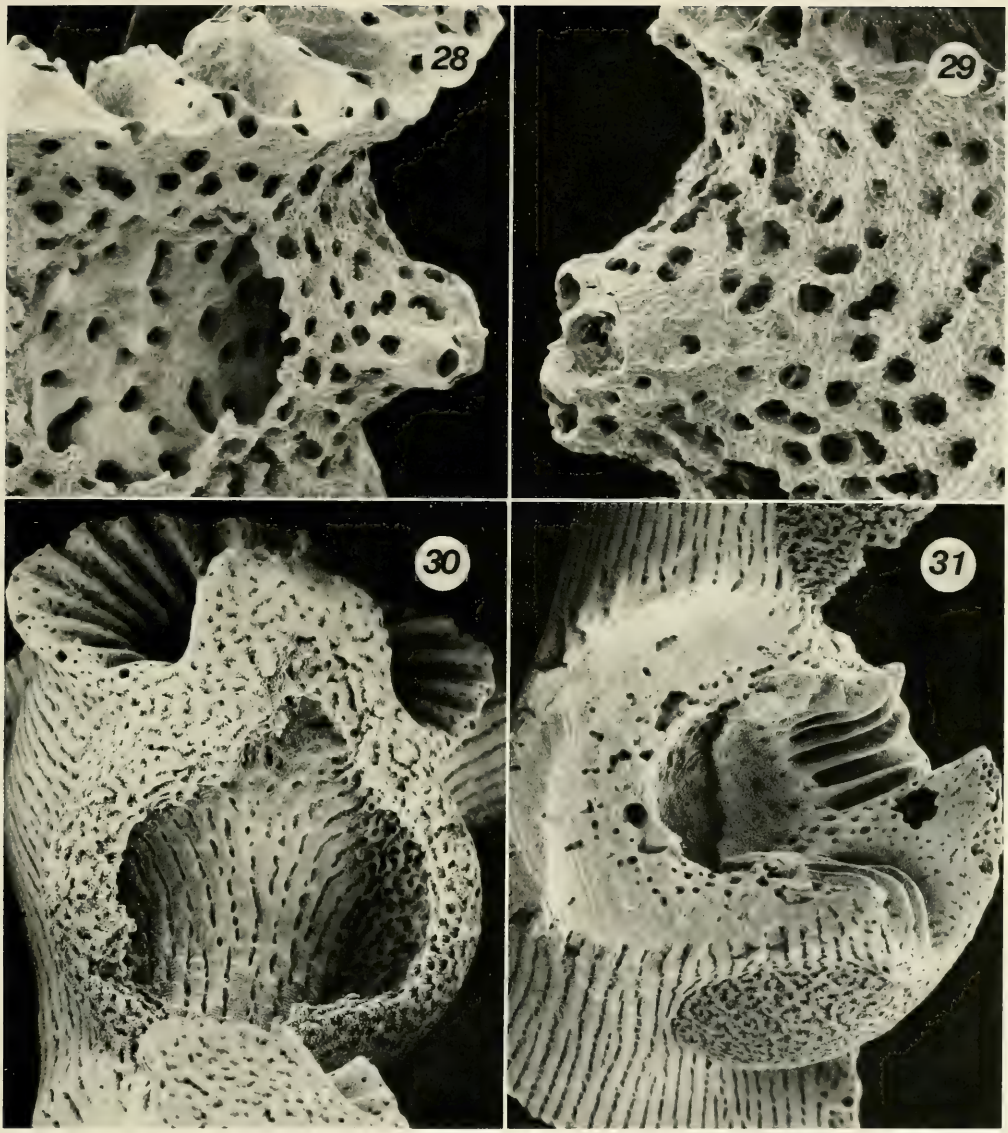
Crypthelia lacunosa Cairns, 1986b:31–33, figs. 20A–G, 21A–C, 27C, G.

New records.—*JSL* Stations 1912, 1 female colony, USNM 84760; 1935, 1 colony, USNM 84761.

Discussion.—Little can be added to the original description, other than that the fe-



Figs. 25–27. 25, *Stylaster cocosensis, JSL*-1944, paratype, USNM 84736: branch segment illustrating female ampullae, cyclosystem, and transition from linear-imbricate to linear-smooth coenosteal texture, ×40, stereo pair; 26, 27, *Stenohelia concinna, JSL*-1929, female colony, USNM 84747: 26, Coenosteal deformation caused by commensal polychaete, ×14.5; 27, Large colony with dozens of polychaete galls, ×0.43.



Figs. 28–31. 28, 29, *Crypthelia eueides, JSL*-1922, USNM 84758: circumferential male ampullae and spiniform processes supporting the efferent pores, ×50, ×64, respectively; 30, 31, *Crypthelia glebulenta, Albatross* 2818, USNM 72104: partially fractured cyclosystem illustrating interior of a female ampulla and an efferent pore on lower side of lid, ×35, ×27.5, respectively.

male colony from *JSL*-1912 is slightly larger than any of the types, measuring up to 8 cm tall and 11 cm broad, with a basal branch diameter of 8.5 mm. The two new records also extend the known bathymetric and geographic distribution of the species.

Distribution.—Off Fernandina, north of Baltra, and southeast of Santa Cruz; 252–806 m; 5.9°–9.0°C.

Crypthelia cymas Cairns, 1986

Crypthelia cymas Cairns, 1986b:33–36, figs. 22A–I, 23A–C, 27H.

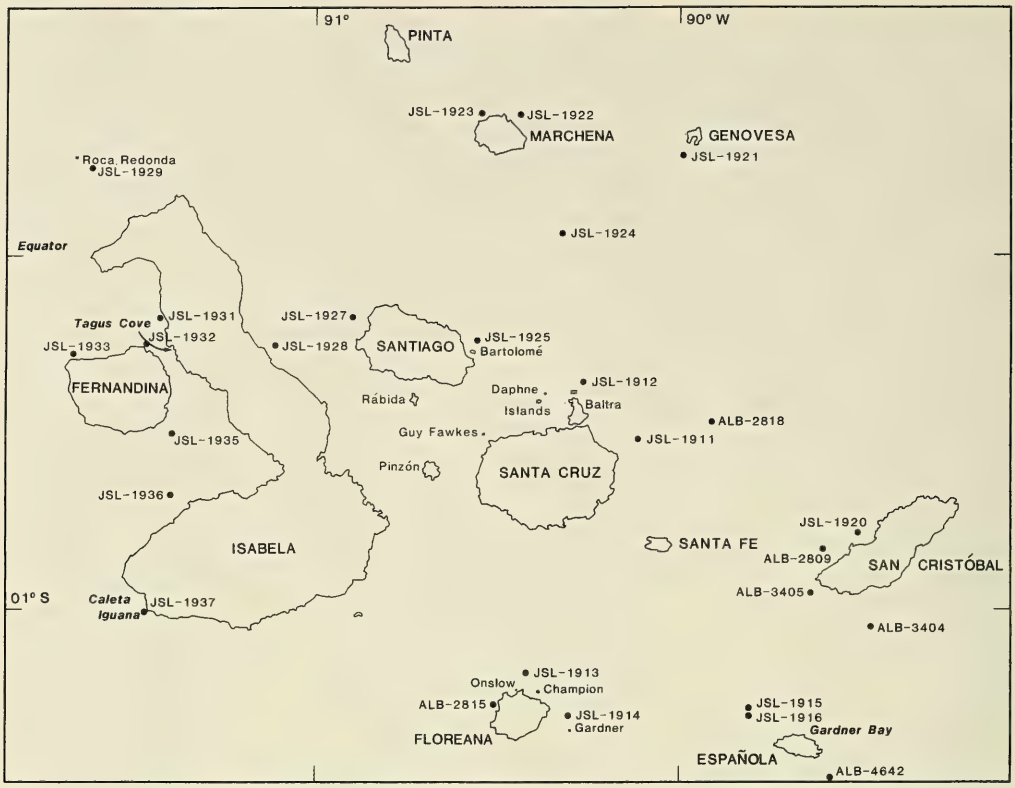


Fig. 32. The Galápagos Islands (excluding the northern-most islands), showing all stations at which stylasterids have been collected.

New records.—*JSL* Stations 1911, female branches, USNM 84765; 1914, 5 female colonies, USNM 84766; 1921, 1 female colony, USNM 84767; 1922, 2 male colonies, USNM 84768; 1923, 4 male colonies, USNM 84769; 1924, 5 male colonies, USNM 84770; 1929, 5 female colonies, USNM 85071; 1937, 1 female colony, USNM 85072.

Discussion.—Identification of male colonies of *Crypthelia* species is customarily easier than that of female colonies, due to the male's more distinctive ampullar morphology. Unfortunately, the females of four of the six Galápagos *Crypthelia* species have the rather nondescript arrangement of "B" (as defined by Cairns 1986b): i.e., ampullae restricted to the proximal cyclosystem wall, which forces reliance on other characters to identify the female colonies. For instance, females of *C. cymas* are very similar to those of *C. glebulenta* in morphology but can be distinguished by having smaller cyclosystems; fewer dactylopores per cyclosystem; and larger, horizontal lids.

Distribution.—Widespread throughout the Galápagos, including off southwest Isabela, Roca Redonda, Marchena, Genovesa, Santa Cruz, and Floreana; off New Zealand (Cairns 1991c); 166–806 m; 5.7°–14.4°C.

Crypthelia dactylopoma Cairns, 1986

Crypthelia dactylopoma Cairns, 1986b:36–41, figs. 24A–H, 25A, B.

New records.—*JSL* Stations 1923, 1 female colony, USNM 85754; 1928, 1 female branch, USNM 84755; 1929, 1 female col-

ony, USNM 84756; 1933, 2 female colonies, USNM 84757.

Discussion.—The small branch fragment from *JSL*-1928 is a typical female specimen, consistent with the original description; however, the colonies from the other three stations differ in having cyclosystems only about half the typical diameter (e.g., about 1.4 mm). Except for the character of cyclosystem size and associated delicacy of the corallum, these specimens are similar to the types.

Distribution.—Off Fernandina, Roca Redonda, Marchena, eastern Isabela, northeast of Santa Cruz, and Española; 348–813 m; 5.0°–10.0°C.

Crypthelia gigantea Fisher, 1938

Cryptohelia [sic] *gigantea* Fisher, 1938:535, pl. 64, fig. 5.
Crypthelia gigantea: Cairns, 1986b:41, figs. 26A–I (synonymy).

New records.—*JSL* Stations 1921, 1 branch, USNM 84751; 1922, 2 female colonies, USNM 84752; 1927, 1 colony, USNM 84753.

Discussion.—Previously known only from the type locality (*Albatross* 2818), *C. gigantea* is herein reported from three additional stations, making possible observations on corallum variation. Branch anastomosis appears to be common, resulting in uniplanar, reticulate flabella. None of the *JSL* specimens were quite as large as the syntypes in cyclosystem diameter (which have the largest cyclosystems of any stylasterid—4.0–4.1 mm in greater diameter [Cairns 1986b]); cyclosystems of the *JSL* specimens ranged from only 2.5 to 3.4 mm in greater diameter. Male cyclosystem lids and nongravid female cyclosystem lids are slightly concave, horizontal, and tongue-shaped, covering 50–70% of the cyclosystem.

Distribution.—Known only from the eastern Galápagos Islands: off Santiago, Marchena, Genovesa, and northeast of Santa Cruz; 475–784 m; 5.6°–8.9°C.

Acknowledgments

The *R/V Seward Johnson/Johnson-Sea-Link I* submersible expedition in 1986 to the Galápagos and Cocos Islands was cosponsored by: Harbor Branch Oceanographic Institution, Inc.; SeaPharm, Inc.; and the National Cancer Institute, Natural Products Branch (Contract N01-CM-67919). I am grateful to co-chief scientists K. L. Rinehart and S. A. Pomponi for the opportunity to participate in this cruise.

I am grateful to Helmut Zibrowius (Station Marine d'Endoume, Marseille) for helpful comments on an early draft of this manuscript. The scanning electron photomicrographs were taken in the SEM Laboratory of the National Museum of Natural History, Smithsonian Institution.

Literature Cited

Boschma, H. 1959. Revision of the Indo-Pacific species of the genus *Distichopora*.—Bijdragen tot de Dierkunde 29:121–171.

———. 1964a. On Stylasaterina of the genus *Stenohelia*.—Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, series C, 67:64–73.

———. 1964. Further notes on the stylasterine coral *Stenohelia concinna*.—Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, series C, 67:74–77.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill Book Co., New York, 475 pp.

Broch, H. 1936. Untersuchungen an Stylasteriden.—Skrifter utgitt av det Norske Videnskaps-Akademi i Oslo, I: Matematisk-naturvidenskapelig Klasse, 1936 (number 8): 103 pp.

———. 1947. Stylasteridae (Hydrocorals) of the *John Murray* expedition to the Indian Ocean.—Scientific Reports of the *John Murray* Expedition 8(2):305–316.

Cairns, S. D. 1983a. Antarctic and Subantarctic Stylasterina (Coelenterata: Hydrozoa).—Antarctic Research Series 38:61–164.

———. 1983b. A generic revision of the Stylasterina (Coelenterata: Hydrozoa). Part 1. Description of the genera.—Bulletin of Marine Science 33: 427–508.

———. 1985. Three new species of Stylasteridae (Coelenterata: Hydrozoa).—Proceedings of the Biological Society of Washington 98:728–739.

———. 1986a. A revision of the Northwest Atlan-

tic Stylasteridae (Coelenterata: Hydrozoa).—Smithsonian Contributions to Zoology 418: 131 pp.

———. 1986b. Stylasteridae (Hydrozoa: Hydroida) of the Galápagos Islands.—Smithsonian Contributions to Zoology 426: 42 pp.

———. 1991a. A revision of the ahermatypic Scleractinia of the Galápagos and Cocos Islands.—Smithsonian Contritutions to Zoology 504: 44 pp.

———. 1991b. A generic revision of the Stylasteridae (Coelenterata: Hydrozoa). Part 3. Keys to the genera.—Bulletin of Marine Science (in press).

———. 1991c. Revision of the Stylasteridae (Cnidaria: Hydroida) from the New Zealand region.—New Zealand Oceanographic Institute Memoir 98 (in press).

Fisher, W. K. 1938. Hydrocorals of the North Pacific Ocean.—Proceedings of the United States National Museum 84:493–554.

Gray, J. E. 1847. An outline of the arrangement of stony corals.—Annals and Magazine of Natural History, series 1, 19:120–128.

Hickson, S. J., & H. M. England. 1905. The Stylasterina of the *Siboga* expedition.—*Siboga* Expedition 8:1–26.

Kent, W. S. 1871. One some new and little-known species of Madrepores, or stony corals, in the British Museum collection.—Proceedings of the Zoological Society of London 1871:275–286.

Marenzeller, E. von. 1904. Stein- und Hydro-Korallen.—Bulletin of the Museum of Comparative Zoology 43:75–87.

Pourtalès, L. F. de. 1867. Contributions to the fauna of the Gulf Stream at great depths.—Bulletin of the Museum of Comparative Zoology 1:103–120.

———. 1868. Contributions to the fauna of the Gulf Stream at great depths (second series).—Bulletin of the Museum of Comparative Zoology 1:121–141.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 229–240

MONOCELIDIDAE (PLATYHELMINTHES: PROSERIATA) FROM PUERTO RICO. I. GENERA *MINONA* AND *MONOCELIS*

Marco C. Curini-Galletti

Abstract.—Three new species of Monocelididae from Puerto Rico are described as *Minona puertoricana, Minona paulmartensi,* and *Monocelis alboguttata. Minona bermudensis* Ax & Sopott-Ehlers, 1985, *Minona gemella* Ax & Sopott-Ehlers, 1985, *Minona peteraxi* Karling, 1978, previously known from Bermuda, and *Monocelis tabira* Marcus, 1950, known from southern Brazil, have also been found in Puerto Rico. Karyotypes are given for all species.

Knowledge on taxonomy and distribution of the family Monocelididae (Platyhelminthes: Proseriata) on the east coast of tropical America is scanty and limited to Bermuda (Ax & Sopott-Ehlers 1985, Karling 1978) and southern Brazil (Marcus 1946, 1949, 1950, 1951, 1954a). Research carried out recently in Puerto Rico resulted in a significant contribution to the knowledge of the group in the Caribbean area; the present first report deals with the genera *Minona* Marcus, 1946 and *Monocelis* Ehrenberg, 1831.

Materials and Methods

Samplings were performed in the proximity of the Marine Biological Station of Isla Magueyes (University of Puerto Rico, Mayaguez) (17°57′N, 67°05′W) in December 1988. Samples were collected by scooping the topmost layer of sediment. Granulometry indices (Md = graphic mean; QDI = Inclusive Graphic Quartile Deviation) are calculated according to Giere et al. (1988).

The following stations were sampled:

St. I: Magueyes Is., moderately sheltered beach among mangroves: a) intertidal, poorly sorted granule (Md = −1.73; QDI = 1.86). Silt-clay fraction: 1.20%. b) Upper subtidal (−20/−30 cm), thin oxidized layer of poorly sorted medium sand (Md = 1.97; QDI = 1.51). Silt-clay fraction: 17.15%.

St. II: Magueyes Is., moderately sheltered beach, upper subtidal (−10 cm). Poorly sorted very coarse sand (Md = −0.46; QDI = 1.26). Silt-clay fraction: 0.91%.

St. III: Magueyes Is., sheltered beach among mangroves; −10/−20 cm. Poorly sorted medium sand (Md = 1.3; QDI = 1.54). Silt-clay fraction: 13.58%.

St. IV: Harbour of La Parguera. Extremely poorly sorted very coarse sand, with appreciable amount of particulated organic matter and oil; about 30 cm deep. Md = −0.81; QDI = 4.07. Silt-clay fraction: 6.53%.

St. V: Caballo Blanco reef, −16 m. Poorly sorted medium sand (Md = 1.4; QDI = 1.28). Silt-clay fraction: 14.62%.

St. VI: Turrumote Cay, exposed beach, intertidal, poorly sorted granule (Md = −1.0; QDI = 1.44). Silt-clay fraction: 0.1%.

St. VII: Turrumote Cay, internal lagoon (connected with the sea at the time of samplings), poorly sorted granule, −20 cm (Md = 1.1; QDI = 1.04). Silt-clay fraction: 0.2%.

St. VIII: Turrumote Cay, channels between rocky and *Montastraea* outcrops, −10 m. Poorly sorted very coarse sand (Md = −0.15; QDI = 1.95). Silt-clay fraction: 0.92%.

Living specimens were isolated with the $MgCl_2$ technique (see Martens 1984). Observations on the anatomy and comparative length of pore indices (a: mouth-vagina; b: vagina-male pore; c1: male pore-accessory organ pore; c2: accessory organ pore-female

pore [or c: male pore-female pore, for species of the genus *Monocelis,* without accessory organ]; d: female pore-caudal tip) (see Karling 1966 and Tajika 1982) were performed on slightly squeezed living specimens. Permanent mountings were done with lactophenol. Types and all collected specimens are deposited in the collection of the Dipartimento di Biomedicina Sperimentale, Infettiva e Pubblica, University of Pisa (BIO).

The karyotype was determined on lactic-acetic orcein stained spermatogonial mitoses, as described by Curini-Galletti et al. (1989). Absolute (a.l.) and relative lengths (r.l. = length of chromosome $\times 100$/total length of the haploid genome) and centromeric indices (c.i. = length of short arm $\times 100$/length of entire chromosome) were obtained from measurements of camera lucida drawings of at least 10 metaphase plates. The idiograms in Fig. 4 are based on absolute lengths; karyometrical data are presented in Table 1. The chromosome nomenclature employed is that of Levan et al. (1964), and the fundamental number (NF) is according to Matthey (1949).

Genus *Minona*

Minona puertoricana, new species

Figs. 1, 4A

Type material.—One whole mount (holotype) (BIO-32).

Type locality.—Harbour of La Parguera, Puerto Rico (St. IV).

Studied material.—About 30 living specimens from stations Ib, II, III, IV. Two whole mounts (holotype, paratype (BIO-33)); 3 specimens used for karyology.

Etymology.—Named after the locality of collection.

Description.—Living worms about 2.3 mm in length, without pigment or eyespots. Cephalic end rounded, provided with ovoidal rhabdoid glands and conspicuous frontal glands. Posterior half of statocyst engulfed into the brain. Caudal end of body bluntly triangular, with numerous adhesive glands and rhabdoid glands similar to cephalic ones plus a few distinctly larger glands. Gut runs from behind brain to tail; tubular pharynx located in second third of body. Behind the pharynx a tranversal septum ("diaphragm") is present.

Approximately 20 testes present, arranged in two rows, anteriorly to pharynx. Copulatory bulb consists of a rather large seminal vesicle, with a diameter of about 55 μm, some prostate glands, and a weak penis papilla. Behind copulatory bulb an accessory organ is present, which has its own pore, and bears an elongated stylet that is 20.3 ± 3.2 μm (12 measurements).

Ovaries in front of pharynx; vitellaria stretch from anterior part to copulatory organs. A rather small bursa, generally rounded in shape, in some specimens more irregular, lies just behind the septum. Vaginal pore discernible in about half the mature specimens. Female duct runs from the bursa dorsally to copulatory bulb and opens caudally through the female pore, which is surrounded by numerous female glands.

Karyotype.—Haploid set made up of two chromosomes, one large metacentric and one small submetacentric with low index value (c.i.: 28.13). Absolute length of haploid genome: 9.3 ± 0.8 μm (Fig. 4A, Table 1).

Ecological notes.—In the upper subtidal of the studied area, *M. puertoricana* is the dominant monocelidid in coarse to medium sand, generally rich in silt-clay fraction, in sheltered conditions (harbours, beaches in mangrove areas); it is absent from dynamic environments. It is the only Proseriate (and indeed one of the few meiofaunal organisms) resistant to severe organic and hydrocarbon pollution in the inner harbor of La Parguera.

Diagnosis.—Unpigmented *Minona* species with four genital openings and an accessory stylet approximately 20 μm long. Pore indices: $b \gg a > d > c2 > c1$. Karyo-

type formula: 2N = 4: 1m + 1sm; haploid genome length: 9.3 μm. NF = 4.

Minona paulmartensi, new species
Figs. 2, 4B

Type material.—One whole mount (holotype) (BIO-46).

Type locality.—Turrumote Cay, Puerto Rico (St. VIII).

Studied material.—Three living specimens, one mounted in lactophenol (holotype), the others used for karyological purposes.

Etymology.—Named after Dr. Paul M. Martens, for his contribution to the study of the Monocelididae.

Description.—A minute (about 1.5 mm) and slender *Minona* species, without pigment or eyespots. Cephalic region rounded, provided with tiny oily droplets in front of statocyst; rhabdoid glands could not be discerned in living specimens both in cephalic and caudal region. Elongated tail provided with numerous adhesive glands. Tubular pharynx located in second third of body.

Approximately 8 testes, in a median row in front of the pharynx. Copulatory bulb markedly ovoidal, consisting of a round seminal vesicle, connected to a barely discernible penis papilla. Longer axis of bulb approximately 50 μm in length. An accessory organ, with its own pore and a stylet about 24 μm long, is situated behind copulatory bulb.

Ovaries in front of the pharynx. Vitellaria stretch from in front of testes to copulatory bulb. Oviducts fuse behind pharynx to form a common oviduct. In front of copulatory bulb this duct widens to form a small, ovoid bursa, provided with a weakly muscular vaginal pore. Common female duct runs over copulatory bulb and opens into the female pore, which is surrounded by female glands.

Karyotype.—Haploid set made up of three chromosomes, the smallest being about ⅔ the length of the largest. Chromosome 1 submetacentric, with a very low centromeric index (c.i: 27.65); chromosomes 2 and 3 subtelocentric. Absolute length of haploid genome: 8.5 ± 0.8 μm (Fig. 4B, Table 1).

Diagnosis.—Unpigmented *Minona* species with four genital openings, with a markedly ovoidal copulatory bulb, and an accessory stylet of about 24 μm. Pore indices: d > a > c1 > b > c2. Karyotype formula: 2N = 6: 1sm + 2st; haploid genome length: 8.5 μm. NF = 4.

Discussion.—Both new species have four genital pores, are unpigmented, and lack eyespots. Other species with this combination of characters are: *M. degadti* Martens, 1983; *M. pelvivaginalis* Tajika, 1982; *M. dolichovesicula* Tajika, 1982; and *M. cornupenis* Karling, 1966. *M. degadti,* from the North Sea, is distinguished by its stylet, which bears a lateral tooth; furthermore, in this species distance b is very short, i.e., the vagina is very close to the male pore. *Minona pelvivaginalis* from Japan has copulatory bulb and accessory organ lying close to each other and in the same plane, has a stylet 30 μm long and 30–40 testes. *Minona dolichovesicula* has been reported from Japan and northwest U.S.A., though these populations are distinct for the length of the accessory stylet (48 μm and 20 μm, respectively). This species is characterized by a large elliptic elongated copulatory bulb, 85 μm in length, surrounded by several layers of muscles. An evident penis papilla is present at its caudal end, and the number of testes is above 30. *Minona cornupenis* from California has a long tubular penis, as long as the bulb, a stylet 30 μm long, a muscular vagina and about 30 testes.

Minona puertoricana and *M. paulmartensi* are easily distinguishable from each other by karyotype, relative position of genital openings, stylet length, and habitat.

Since the vagina often develops late or is lacking in certain maturity stages (Karling 1966; and see under *M. puertoricana*), species originally described as without a vagina should be taken into consideration for dis-

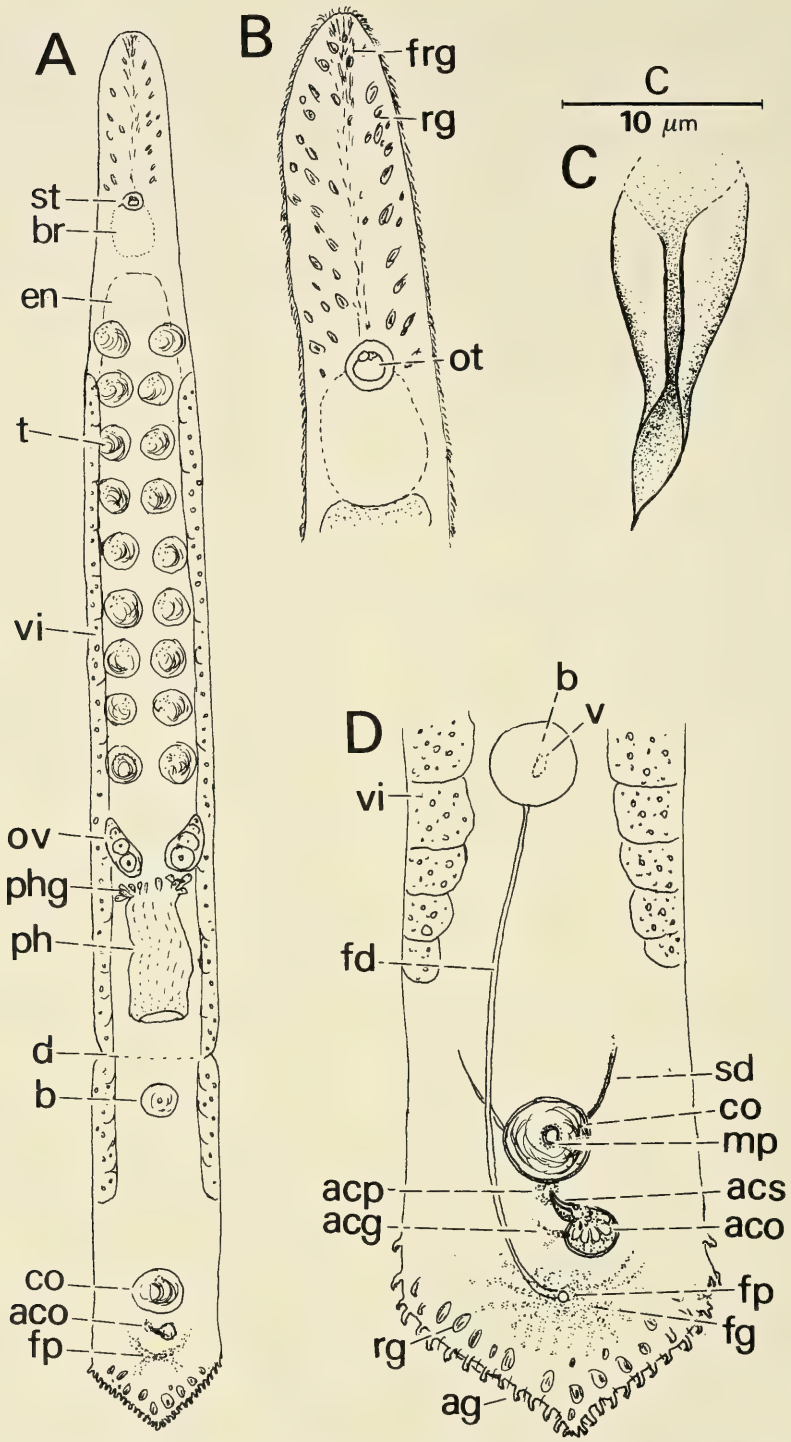


Fig. 1. *Minona puertoricana*: A, General organization, from a living animal in dorsal view; B, Details of the cephalic region; C, Accessory stylet from a whole mount; D, Genital organs in a living animal. *Acg*; accessory organ glands; *aco*: accessory organ; *acp*: accessory organ pore; *acs*: accessory organ stylet; *ag*: adhesive glands;

cussion. These are: *M. baltica* Karling & Kinnander, 1953; *M. obscura* Karling, 1966; *M. bermudensis* Ax & Sopott-Ehlers, 1985; *M. fernandinensis* Ax & Ax, 1977; *M. indonesiana* Martens & Curini-Galletti, 1989; and *M. beaglei* Martens & Curini-Galletti, 1989. *Minona baltica* is a brackish-water species from northern Europe and eastern Canada; it has a large stylet, being 40–50 μm long. *Minona obscura,* from California, has two pigmented eyes and brown pigment in the parenchyma. *Minona bermudensis* has 60–65 testes, very large squarish bursa, a stylet of 25–28 μm, and, at least in the Puerto Rico specimens attributed to this species, a fused male pore-accessory organ pore (see below). *Minona fernandinensis,* from the Galápagos, has 80–90 testes and a stylet of 35–38 μm. *Minona indonesiana,* from Sulawesi, lacks a bursa, has a large male antrum, and a stylet of 30–32 μm. *Minona beaglei,* from northern Australia, has a bursa consisting of several distinct vesiculae. *Minona hastata* Martens & Curini-Galletti, 1989, from Sulawesi, whose number of genital openings could not be established, has a very long (70 μm) accessory stylet.

The condition with four genital openings is considered as the plesiomorphic state within the genus *Minona* (Ax & Sopott-Ehlers 1985); since the two new species do not appear to share any synapomorphy with any other known species of the genus, their phylogenetic position cannot be determined at the moment.

Minona bermudensis Ax & Sopott-Ehlers, 1985

Minona bermudensis Ax & Sopott-Ehlers, 1985:377–379.—Martens & Curini-Galletti, 1989:185.

Studied material.—Four specimens (St. Ia).

Distribution.—Bermuda (Shelly Bay, Whalebone Bay) (Ax & Sopott-Ehlers 1985); Puerto Rico (Magueyes Is.).

Karyotype.—Haploid set made up of three chromosomes, almost of the same size. Chromosome 1 metacentric; chromosomes 2 and 3 submetacentric. Absolute length of haploid genome: 7.3 ± 0.7 μm. NF = 6 (Fig. 4D, Table 1).

Remarks.—Specimens from Puerto Rico correspond to the original description of *M. bermudensis* with respect to the number of testes, presence of a broad squarish bursa, stylet size (Bermuda: 25–28 μm; Puerto Rico: 28.72 ± 2.36 μm, $n = 4$), and general topography of the copulatory organs. In the original description the number of genital openings is not given; in specimens from Puerto Rico a vagina was not observed, and the male copulatory organ and the accessory organ had a large common opening. Specimens from both Bermuda and Puerto Rico were found in coarse, littoral sediments.

Minona peteraxi Karling, 1978

Minona peteraxi Karling, 1978:226–228.—Martens, 1983:154–155.—Sopott-Ehlers & Ax, 1985:340.

Studied material.—Two specimens (St. VI).

Distribution.—Bermuda (several places around the Biological Station) (Karling 1978); Puerto Rico (Turrumote Cay).

Karyotype.—Haploid set made up of three chromosomes, the smallest being nearly ⅔ the length of the largest. Chromosomes 1 and 3 submetacentric; chromosome 2 metacentric. Absolute length of haploid genome: 10.5 ± 1.0 μm. NF = 6 (Fig. 4E, Table 1).

←

b: bursa; *br*: brain: *co*: copulatory organ; *d*: diaphragm; *e*: eye; *en*: enteron; *fd*: female duct; *fg*: female glands; *fp*: female pore; *frg*: frontal glands; *mp*: male pore; *o*: oily droplets; *od*: oviduct; *ov*: ovary; *ot*: otolith; *ph*: pharynx; *phg*: pharyngeal glands; *pi*: pigment; *rg*: rhabdoid gland; *sd*: seminal duct; *st*: statocyst; *t*: testes; *v*: vaginal pore; *vi*: vitellary.

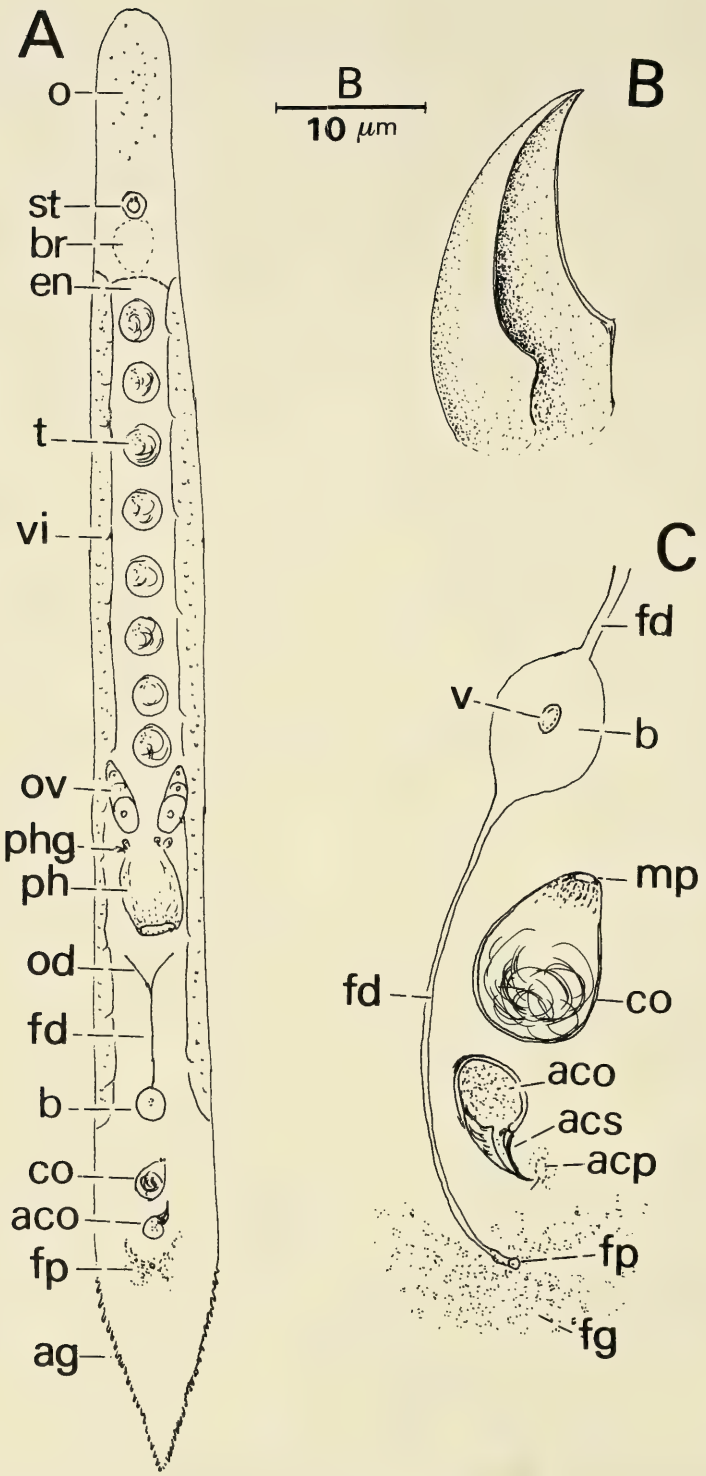


Fig. 2. *Minona paulmartensi*: A, General organization, from a living animal in dorsal view; B, Accessory stylet, from a whole mount; C, Genital organs in a living animal.

Remarks.—A highly characteristic species because of its peculiar pigmentation, eyes at the extreme anterior tip, and paired vaginae. This species has a broad ecological spectrum in Bermuda (fine sand, sand with mud, sand with gravel, on algae and hydroids) (Karling 1978), whereas in Puerto Rico it has been found only in granule, almost devoid of silt-clay fraction, in shallow water.

Minona gemella
Ax & Sopott-Ehlers, 1985

Minona gemella Ax & Sopott-Ehlers, 1985: 375–377.

Studied material.—Thirty-one specimens (St. VI, VII).

Distribution.—Bermuda (Long Bay, Mylords Bay) (Ax & Sopott-Ehlers 1985); Puerto Rico (Turrumote Cay).

Karyotype.—Haploid set made up of two chromosomes, the smallest nearly ⅔ the size of the largest. Both chromosomes metacentric; chromosome 1, however, is nearly at the border with the submetacentric class. Absolute length of haploid genome: 6.3 ± 0.4 μm. NF = 4 (Fig. 4E, Table 1).

Remarks.—This species is characterized by the presence of two accessory organs, one (rostral) in front and one (caudal) behind the copulatory organ. According to the original description (Ax & Sopott-Ehlers 1985), the rostral accessory organ joins the vagina to form a common pore; nothing could be stated for the other pores. In the Puerto Rico specimens, a common vagina + rostral accessory organ pore could not be detected; the male copulatory organ and the caudal accessory organ joined to form a large common pore; the female pore was distinct. There were over 50 testes in the Puerto Rico animals, about 20 in Bermuda specimens. The stylet of the caudal accessory organ is described by Ax & Sopott-Ehlers (1985) as broader and less curved than the rostral accessory organ stylet; their lengths are 30 μm and 25 μm, respectively. In specimens from Puerto Rico the two stylets were similar in shape and length, attaining sizes of 33.5 ± 9.9 μm (range 22.6–50.7 μm) and 32.3 ± 14.2 μm (range 22.0–53.6 μm) (n = 14), respectively. The species appears exceedingly variable in Puerto Rico as far as stylet length is concerned; furthermore, about half of the specimens lacked the rostral accessory organ. It is not clear whether this structure is attained only at maturity; the specimens examined had no evident signs of immaturity.

Minona gemella was found in Bermuda in medium to coarse sand; in Puerto Rico it is restricted to areas of granule, almost without silt-clay fraction.

Genus *Monocelis*
Monocelis alboguttata, new species
Figs. 3, 4F

Type material.—One whole mount (BIO-20).

Type locality.—Caballo Blanco reef, 16 m (St. V).

Studied material.—Three specimens, one mounted in lactophenol (holotype), the others used for karyology.

Etymology.—From latin *albus* (white) and *gutta* (drop); it refers to the peculiar cephalic pigmentation.

Description.—Living worms about 2 mm in length, without pigmented eyes. Cephalic area in front of statocyst scattered with numerous small pigmented dots, which are white in reflected, black in transmitted light. They are irregularly arranged and variable in the three specimens found. Caudal region somewhat elongated, with numerous adhesive glands and tiny rhabdoid glands. Pharynx slightly longer than wider, located in second third of body.

Between 14–20 testes present. Globular copulatory bulb about 70 μm in diameter, with an ill-defined penis papilla. In front of penial papilla, a sphaerical bursa is located, similar in size to copulatory bulb, with distinct, rounded, wide vagina. A straight fe-

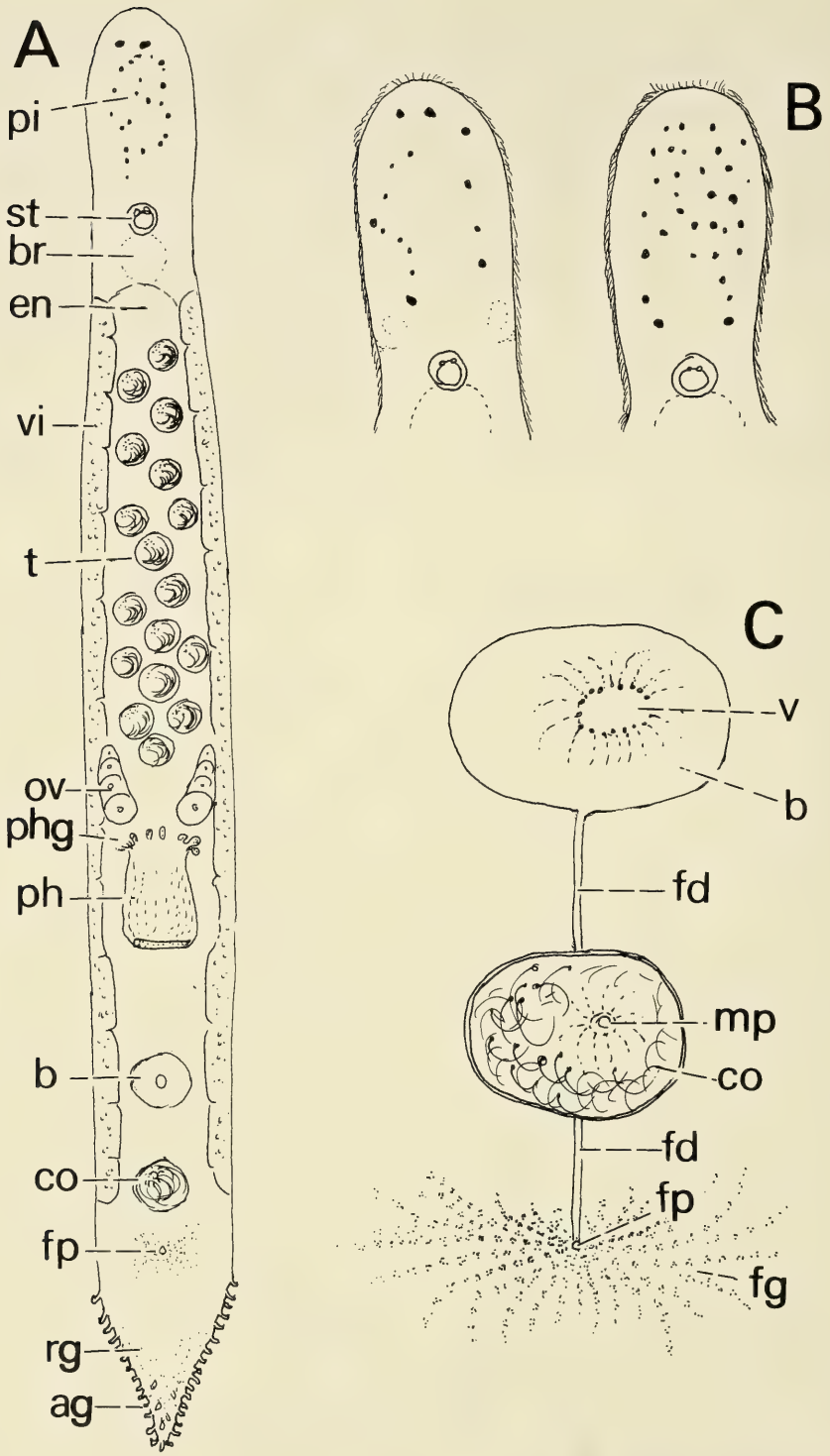


Fig. 3. *Monocelis alboguttata*: A, General organization, from a living animal in dorsal view; B, Cephalic region in two specimens; C, Genital organs in a living animal.

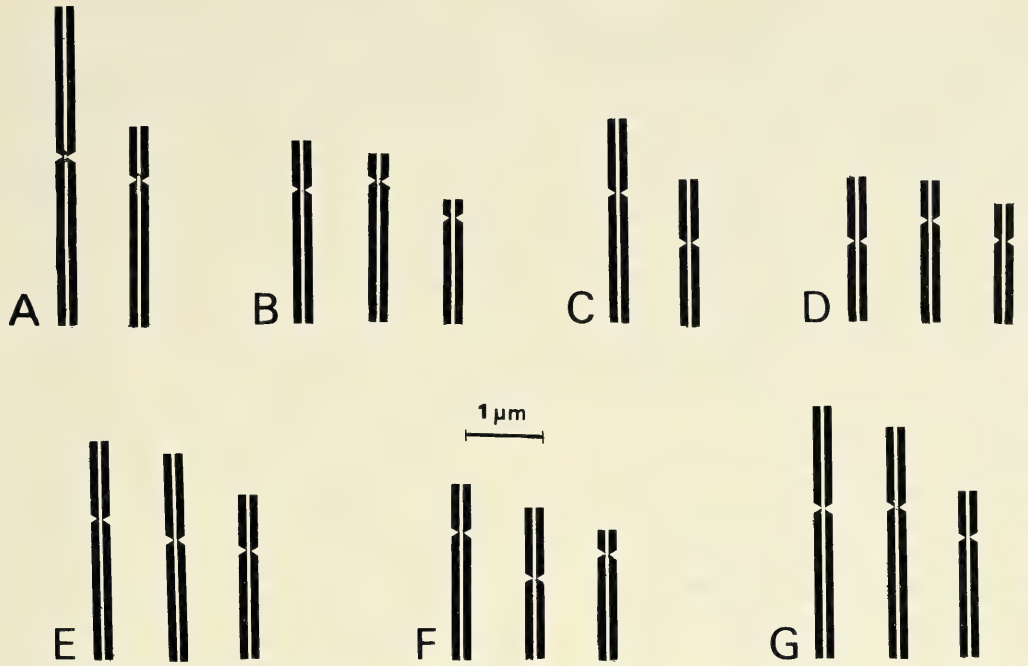


Fig. 4. Idiograms (based on absolute lengths) representing the haploid sets of *Minona puertoricana*: (A), *Minona paulmartensi* (B), *Minona gemella* (C), *Minona bermudensis* (D), *Minona peteraxi* (E), *Monocelis alboguttata* (F), and *Monocelis tabira* (G).

male duct was seen departing from the bursa; posterior to copulatory bulb the female duct opens into a female pore, which is surrounded by glands.

Karyotype.—Haploid set made up of three chromosomes, the smallest almost ⅔ the length of the largest. Chromosome 1 subtelocentric, bordering at submetacentric (c.i.: 24.98); chromosome 2 metacentric; chromosome 3 subtelocentric. Absolute length of haploid genome: 8.2 ± 1.1 µm (Fig. 4F, Table 1).

Diagnosis.—*Monocelis* species without eyes and with numerous pigmented dots in front of the statocyst. With three genital openings; bursa and copulatory bulb approx. the same size. Pore indices: d > a > b = c; Karyotype formula: 2N = 6: 1m + 2st; haploid genome length: 8.2 µm. NF = 4.

Discussion.—The systematics of the genus *Monocelis* is complex due to the large number of very similar species. In addition to the new species, species devoid of pigmented eyes and with a vagina are: *M. balanocephala* (Bohming, 1902); *M. cincta* Karling, 1966; *M. tenella* Karling, 1966; *M. hopkinsi* Karling, 1966; *M. colpotriplicis* Tajika, 1982; and *M. spectator* Sopott-Ehlers & Ax, 1985.

Monocelis balanocephala, from the Magellan Strait area, has paired vaginae. In all the other species, except the new species, the vagina is situated far from the male pore, pore index b having the highest value. Furthermore, *M. colpotriplicis* from Japan has a bursa much smaller than the copulatory bulb and a distinctly muscular penis; *M. cincta,* from California, has a brown transversal pigment girdle in front of the statocyst; *M. tenella* from California has a distinct male antrum, and its cephalic region is packed with short rod-shaped rhabdites, whereas they are long, needle shaped, in *M. hopkinsi* from California and *M. spectator*

Table 1.—Karyometric data (means ± *SD*) of the haploid complements of *Minona* and *Monocelis* species from Puerto Rico. Nomenclature: m = metacentric; sm = submetacentric; st = subtelocentric.

	Chromosome			Haploid genome length (μm)
	1	2	3	
Minona puertoricana, new species				
a.l. (μm):	5.7 ± 0.4	3.5 ± 0.4		
r.l.:	61.81 ± 1.80	38.19 ± 1.80		9.3 ± 0.8
c.i.:	47.19 ± 1.49	28.13 ± 3.93		
Nomenclature:	m	sm		
Minona paulmartensi, new species				
a.l. (μm):	3.2 ± 0.3	3.0 ± 0.3	2.2 ± 0.3	
r.l.:	37.92 ± 1.84	36.08 ± 1.34	25.99 ± 1.34	8.5 ± 0.8
c.i.:	27.65 ± 4.89	16.50 ± 2.16	16.81 ± 4.29	
Nomenclature:	sm	st	st	
Minona peteraxi				
a.l. (μm):	3.9 ± 0.5	3.7 ± 0.3	2.9 ± 0.3	
r.l.:	37.03 ± 1.70	35.21 ± 1.47	27.76 ± 2.35	10.5 ± 1.0
c.i.:	35.04 ± 2.98	40.91 ± 1.86	32.71 ± 3.39	
Nomenclature:	sm	m	sm	
Minona bermudensis				
a.l. (μm):	2.6 ± 0.3	2.5 ± 0.2	2.2 ± 0.2	
r.l.:	35.45 ± 1.71	34.30 ± 1.55	30.19 ± 1.79	7.3 ± 0.7
c.i.:	44.90 ± 2.56	28.56 ± 6.03	33.77 ± 4.71	
Nomenclature:	m	sm	sm	
Minona gemella				
a.l. (μm):	3.7 ± 0.2	2.6 ± 0.2		
r.l.:	58.66 ± 1.59	41.34 ± 1.59		9.5 ± 1.5
c.i.:	37.74 ± 3.48	44.95 ± 2.34		
Nomenclature:	m	m		
Monocelis alboguttata, new species				
a.l. (μm):	3.1 ± 0.5	2.7 ± 0.2	2.3 ± 0.4	
r.l.:	38.14 ± 1.81	34.14 ± 2.28	27.70 ± 2.36	8.2 ± 1.1
c.i.:	24.98 ± 5.42	45.48 ± 1.31	15.10 ± 6.65	
Nomenclature:	st	m	st	
Monocelis tabira				
a.l. (μm):	4.5 ± 0.4	4.1 ± 0.5	3.0 ± 0.3	
r.l.:	38.78 ± 2.09	35.31 ± 2.15	25.92 ± 1.43	11.6 ± 1.1
c.i.:	39.98 ± 2.11	34.51 ± 3.57	26.88 ± 4.45	
Nomenclature:	m	sm	sm	

from Washington. In addition, the pigmentation of *M. alboguttata* is unique among the Monocelididae.

Karyotypes of some *Monocelis* species are known (Martens & Curini-Galletti 1987). *Monocelis alboguttata* has a slightly modified basic karyotype for the genus, because of pericentric inversions.

Since a phylogenetic revision of the genus *Monocelis,* taking into account morphological and karyological data, has yet to come, the relationships of the new species cannot be determined at present.

Monocelis tabira Marcus, 1950

Monocelis tabira Marcus, 1950:54–56.—Westblad, 1952:33–34.—Marcus, 1954b:

32.—Karling, 1966:505.—Ax & Ax, 1977: 14–15.

Studied material.—Six specimens (St. Ib, II and III).

Distribution.—Brazil (Baia de Santos, Sao Sebastiao Is., Rio de Janeiro) (Marcus 1950); Puerto Rico (Magueyes Is.). Westblad's (1952) attribution to this species of specimens from the Falkland Is. is dubious (see Karling 1966 and Marcus 1954b).

Karyotype.—Haploid set made up of three chromosomes, the smallest nearly ⅔ the size of the largest. Chromosome 1 metacentric; chromosomes 2 and 3 submetacentric. Absolute length of haploid genome: 11.6 ± 1.1 μm. NF = 6 (Fig. 4G, Table 1).

Remarks.—Marcus (1950) did not report the existence of any rhabdoid cells in the cephalic area of *M. tabira,* which contrasts with the very small dot-like rhabdoids present in the Puerto Rico specimens. However, these rhabdoids are possibly not easily appreciable in sections, while the Puerto Rico specimens agree in any other respect with Marcus's description of *M. tabira.* The high value of the genome size is distinctive within the genus *Monocelis* (see Martens & Curini-Galletti 1987) and is probably an apomorphic character for the species.

Acknowledgments

Dr. Prof. Douglas Y. Shapiro provided working facilities at his laboratory at Isla Magueyes; he and Milbrey Leighton are also thanked for their hospitality. Angie McGehee, Shawna Reed, Melody Roy, and students and members of the Principia College (Elsah, Illinois) are thanked for their assistance during dives and samplings.

Literature Cited

Ax, P., & R. Ax. 1977. Interstitielle fauna von Galapagos XIX. Monocelididae (Turbellaria, Proseriata).—Mikrofauna des Meeresbodens 64: 397–438.

———, & B. Sopott-Ehlers. 1985. Monocelididae (Plathelminthes, Proseriata) von Bermuda.—Microfauna Marina 2:371–382.

Curini-Galletti, M. C., I. Puccinelli, & P. M. Martens. 1989. Karyometrical analysis of 10 species of the subfamily Monocelidinae (*Proseriata, Platyhelminthes*) with remarks on the karyological evolution of the Monocelididae.—Genetica 78: 169–178.

Giere, O., A. Eleftheriou, & D. J. Murison. 1988. Abiotic factors. Pp. 61–78 *in* R. P. Higgins and H. Thiel, eds., Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, D.C.

Karling, T. G. 1966. Marine Turbellaria from the Pacific coast of North America IV. Coelogynoporidae and Monocelididae.—Arkiv fur Zoologi 18:493–528.

———. 1978. Anatomy and systematics of marine Turbellaria from Bermuda.—Zoologica Scripta 7:225–248.

Levan, A., K. Fredga, & A. A. Sandberg. 1964. Nomenclature for centromeric position on chromosomes.—Hereditas 52:201–220.

Marcus, E. 1946. Sobre Turbellaria Brasileiros.—Boletim da Faculdade de Filosofia, Ciencias e Letras, Universidade São Paulo (Zoologia) 11:5–254.

———. 1949. Turbellaria Brasileiros (7).—Boletim da Faculdade de Filosofia, Ciencias e Letras, Universidade São Paulo (Zoologia) 14:7–156.

———. 1950. Turbellaria Brasileiros (8).—Boletim da Faculdade de Filosofia, Ciencias e Letras, Universidade São Paulo (Zoologia) 15:5–192.

———. 1951. Turbellaria Brasileiros (9).—Boletin da Faculdade de Filosofia, Ciencias e Letras, Universidade São Paulo (Zoologia) 16:5–216.

———. 1954a. Turbellaria Brasileiros (11).—Papeis Avulsos, Departmento de Zoologia, São Paulo 11:419–489.

———. 1954b. Reports of the Lund University Chile Expedition 1948–49. 11. Turbellaria.—Kungl. Fysiografiska Sällskapets Handlingar. N.F. 64(13):1–115.

Martens, P. M. 1983. Three new species of Minoninae (Turbellaria, Proseriata, Monocelididae) from the North Sea, with remarks on the taxonomy of the subfamily.—Zoologica Scripta 12 (3):153–160.

———. 1984. Comparison of three different extraction methods for Turbellaria.—Marine Ecology Progress Series 14:229–234.

———, & M. C. Curini-Galletti. 1987. Karyological study of three *Monocelis*-species, and description of a new species from the Mediterranean, *Monocelis longystila* sp.n. (Monocelididae, Plathelminthes).—Microfauna Marina 3:297–308.

———, & ———. 1989. Monocelididae and Archimonocelididae (Platyhelminthes Proseriata) from South Sulawesi (Indonesia) and Northern

Australia with biogeographical remarks.—Tropical Zoology 2:175–205.

Matthey, R. 1959. Les chromosomes des Vertébrés. Rouge, Lausanne, 344 pp.

Sopott-Ehlers, B., & P. Ax. 1985. Proseriata (Plathelminthes) von der Pazifikkuste der USA (Washington). III. Monocelididae.—Microfauna Marina 2:331–346.

Tajika, K. J. 1982. Marine Tubellarien aus Hokkaido, Japan IX. Monocelididae (Proseriata).—Bulletin Liberal Arts & Science Course, Sch. Med. Nihon University 10:10–34.

Westblad, E. 1952. Turbellaria (excl. Kalyptorhynchia) of the Swedish South Polar expedition 1901–1902.—Further Zoological Results of the Swedish Antarctic Expedition 4(8):1–55.

Dipartimento di Scienze dell'Ambiente e del Territorio, Universita' di Pisa, via Volta 6, I-56100 Pisa, Italy.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 241–246

ARENE BOUCHETI, A NEW INTERTIDAL LIOTIINE TURBINID (MOLLUSCA: GASTROPODA: TROCHOIDEA) FROM TRINDADE ISLAND, SOUTH ATLANTIC OCEAN

José H. Leal

Abstract.—The turbinid *Arene boucheti,* new species, is described from the rocky intertidal of the oceanic Trindade Island, located 1100 km off the Brazilian coast. Shell, opercular and radular characters allocate *A. boucheti* in the subfamily Liotiinae. The endemic species is characterized by a depressed, small but heavy shell with nodulose sculpture, coloration of grayish-green radial flamules and thick, strongly prosocline aperture.

Resumo.—O turbinideo *Arene boucheti* sp. n. é descrito. A nova espécie é proveniente do mesolitoral rochoso da Ilha da Trindade, situada a 1100 km ao largo da costa brasileira. Caracteres da concha, opérculo e rádula indicam que *A. boucheti* pertence à subfamília Liotiinae. A espécie endêmica é caracterizada por uma concha deprimida, pequena e sólida, com escultura nodulosa, coloração de faixas radiais verde-acinzentadas, com abertura espêssa, marcadamente prosoclínea.

During the cruise MD55 made in May 1987 by the French research ship *Marion-Dufresne,* an undescribed turbinid was collected alive underneath volcanic boulders in the rocky shore of southeastern Trindade Island. In a similar fashion to several eastern Pacific liotiines (McLean 1970a, 1970b, 1971), but unlike species from the western Atlantic (Abbott 1974, Leal & Coelho 1985, McLean et al. 1988, Rios 1985), individuals of the new species live in the intertidal zone.

A distance of 1100 km separates Trindade Island from the nearest continental mass, the coast of eastern Brazil (Fig. 1). Trindade and the tiny islets of the Martin Vaz Archipelago, 50 km to the east, are the emerged and most recent expressions of a tectonic hotspot (Morgan 1983). Because of the relative ease in detecting the species due to aggregation of individuals in the rocky intertidal habitat, it is evident that the species is absent from the Brazilian coast, and endemic from Trindade. The species was not collected in a large number of sublittoral stations made in Trindade, Martin Vaz, and on top of the submerged seamounts of the Vitória-Trindade Seamount Chain during the cruise MD55 (Leal & Bouchet 1991). Specimens examined are deposited in the following institutions: Los Angeles County Museum of Natural History (LACM); Museu de Zoologia, Universidade de São Paulo (MZUSP); Museu Oceanográfico de Rio Grande (MORG); Muséum national d'Histoire Naturelle, Paris (MNHN).

Family Turbinidae Rafinesque, 1815
Subfamily Liotiinae H. & A. Adams, 1854
Genus *Arene* H. & A. Adams, 1854
Arene boucheti, new species
Figs. 2–12, 15–17

Description.—Shell depressed-turbinate, thick-walled, small for genus, reaching 3.6 mm height and 3.9 mm width, opaque-white with radiating grayish-green flamules, 8 flamules in final whorl (Figs. 2–7). Intensity of color flamules vary in different specimens. Periostracum undetectable. Protoconch

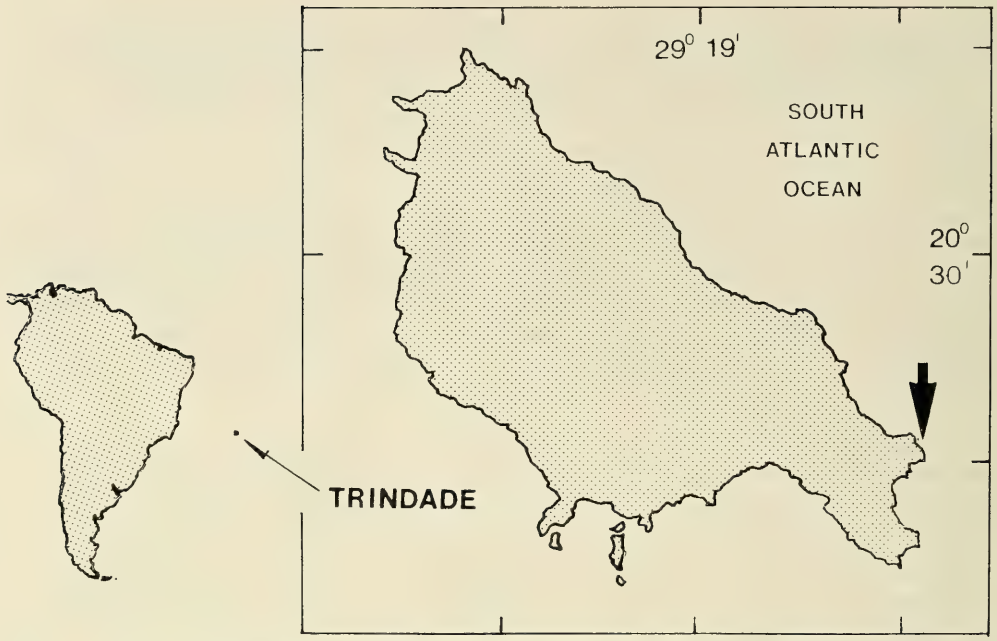
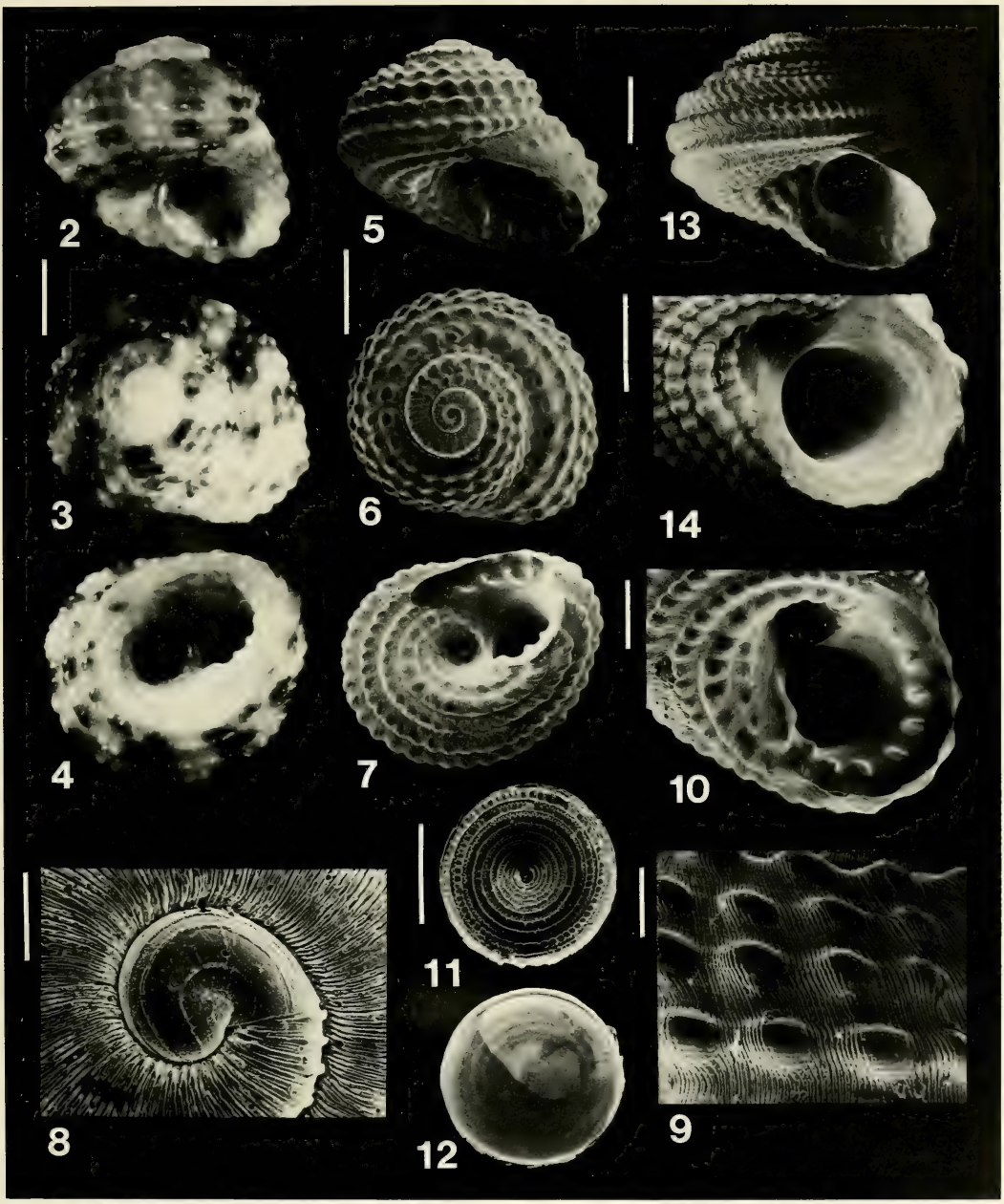


Fig. 1. Location of Trindade Island in the south Atlantic Ocean and of the type locality of *Arene boucheti* new species in Trindade Island (arrow).

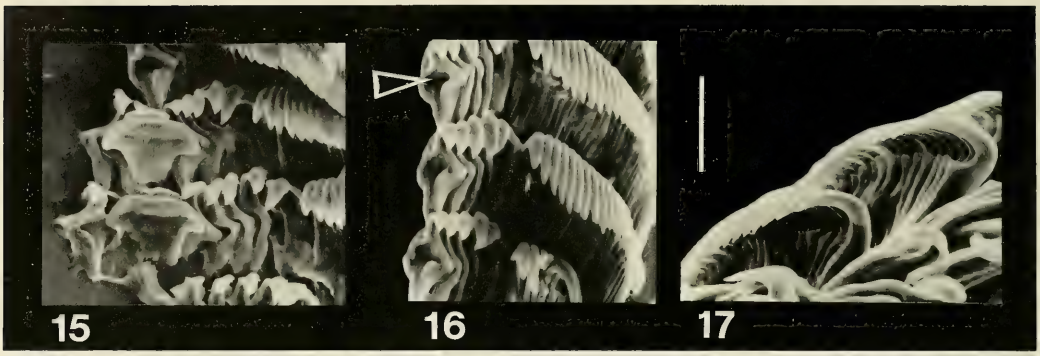
white, 1.5 whorls, 0.25 mm diameter (Fig. 8). Apical surface of protoconch sculptured with 3 fine, well-defined spiral threads. Transition protoconch/teleoconch slightly flared. Teleoconch with 3.25 whorls. Spiral sculpture of five nodulose cords present only after 1.5 teleoconch whorls, 24–32 nodules/cord in final whorl. Adapical cord in each whorl slightly broader than others. Abapical cord in final whorl delimits both periphery and base. Axial sculpture of fine lamellae present over entire teleoconch surface (Fig. 9). Approximately 60 axial lamellae/mm in final whorl. Suture channeled. Base with 4 nodulose spiral cords, third cord wider than other 3, fourth and most abapical cord bordering the umbilicus (Figs. 7, 10). Umbilicus well-defined, deep. Aperture circular, strongly prosocline, thick, with 9 rounded denticles on outer lip, adapical extremity of external lip projecting over base (Fig. 10). Operculum circular, reaching 2.0 mm diameter, multispiral (Figs. 11, 12). Outer surface concave with central depression and about 12 spiral rows of calcareous nodules. Inner surface convex, chitinous. Opercular attachment scar large, situated abaxially.

Radula.—Rhipidoglossate, formula $\infty + 5 + 1 + 5 + \infty$. Rachidian tooth broad, cuspless, with wide cutting edge. Lateral teeth single-cusped, external edges serrate (Figs. 15, 16). Lateral expansions of rachidian tooth interlock in ball-and-socket fashion with depressions in inner base of first lateral teeth (Fig. 16, arrow). Depression in inner base of each lateral tooth forms projection in its outer base. Projection interlocks with corresponding depression in next lateral tooth. Process is repeated in all lateral teeth. Marginal teeth with single, sickle-like cusps (Fig. 17). Cusps prominent and strongly hooked in inner marginal teeth, becoming externally serrated and progressively finer in outer marginal teeth. Single secondary cusps present internally on inner marginals.

Etymology.—Named after my colleague Philippe Bouchet of the Muséum national d'Histoire Naturelle, Paris, France, who first noticed this species in Trindade Island.



Figs. 2–14. 2–4: *Arene boucheti* new species, holotype: 2, Apertural view; 3, Apical view; 4, Umbilical view. Scale bar equals 1 mm. 5–12: *Arene boucheti* new species, SEM micrographs of paratype 1: 5, Apertural view; 6, Apical view; 7, Umbilical view. Scale bar equals 1 mm; 8, protoconch. Scale bar equals 0.1 mm; 9, Detail of shell surface at final whorl. Scale bar equals 0.2 mm; 10, Detail of aperture and umbilicus; 11, External surface of operculum; 12, Internal surface of operculum with attachment scar. (Note that Fig. 5 shows slight SEM distortion—shell is more depressed when compared to the photomicrograph in Fig. 2). Scale bars (10–12) equal 0.5 mm. 13, 14: *Arene guttata* McLean, 1970, SEM micrographs, Isla Santa Cruz, Galápagos Islands: 13, Apertural view; 14, Detail of aperture and umbilicus. Scale bars equal 1 mm.



Figs. 15–17. *Arene boucheti* new species, SEM micrographs of radula: 15, Half rows showing rachidian and lateral teeth; 16, Half rows showing sockets in first lateral teeth (arrow) where projection of rachidian teeth interlock; 17, Marginal teeth. Scale bar equals 0.02 mm.

Type locality.—Southeastern coast of Trindade Island, between Ponta das Tartarugas and Ponta do Túnel, 20°31′S, 29°18′W, in tide pool (see Fig. 1 [arrow], and Diretoria de Hidrografia e Navegação [1985] for details).

Holotype.—MZUSP 27816, 3.44 mm height, 3.75 mm width, live-collected at type locality, under boulders of volcanic rock during low tide, P. Bouchet and J. H. Leal, 22 May 1987.

Paratypes.—MORG 25621, 1 shell; MNHN, 5 live-collected specimens; all from type locality. For shell measurements see Table 1.

Remarks.—The new species is very distinctive in shell morphology from the type species of *Arene* (*Turbo cruentatus* Mühlfeld, 1829), which is large-shelled, with a stellate periphery. It is closer in profile to the western Atlantic *Marevalvata* Olsson & Harbison, 1953, but lacks the flat base of the type species (*Architectonica tricarinata* Stearns, 1872) (see descriptions in Olsson & Harbison 1953). The generic allocation of *A. boucheti* tentatively follows the broad sense used by previous workers for this genus (Olsson & Harbison 1953; McLean 1970a, 1970b, 1971).

Table 1.—Shell measurements of holotype and 6 paratypes of *Arene boucheti* new species. Measurements in mm.

Character	Range	Mean	*SD*
Height	3.00–3.56	3.20	0.21
Width	3.34–3.88	3.60	0.20
Height final whorl	1.44–2.19	1.81	0.24
Aperture diameter	1.63–1.94	1.76	0.11
Protoconch diameter	0.23–0.29	0.25	0.02
Nodules/cord final whorl	24–32	27.4	2.6

Marked radular similarities and resemblance in shell morphology suggested comparison of the new species to the liotiine genus *Cinysca* Kilburn, 1970 (see Barnard 1963, Kilburn 1970). *Cinysca,* however, is restricted to southern Africa, and differs from all other liotiines by having sexually dimorphic shells—females have larger umbilical cavities where they brood the larvae (J. H. McLean, in litt.).

Radular similarities are not restricted to *Arene,* s.l., and *Cinysca.* The similarity of radulae of liotiines and homalopomatines has been mentioned by McLean (1987) and is thoroughly discussed in the suprageneric arrangement proposed by Hickman & McLean (1990) for the Trochoidea. Hickman (1984) provided SEM micrographs of homalopomatine radulae quite similar to that in *A. boucheti,* and observed that, in radular rows of *Homalopoma carpenteri* (Pilsbry 1888), "basal interactions involve both overlap and interlock," very much like what occurs in the new species. The same pattern

is found at least in another trochacean family: Marshall (1988) gave SEM micrographs of the radula in the original description of the deep-sea skeneid *Dillwynella lignicola* Marshall, 1988. A broad rachidian tooth is present, wider in the middle section; lateral teeth have interlocked bases, and the marginal teeth are elongate, sickle-shaped.

Arene boucheti is related in general shell morphology to *A. guttata* McLean, 1970 from the Galápagos Islands (Figs. 13, 14) (LACM 145166, 5 shells, Isla Santa Cruz [Indefatigable], Galápagos, J. de Roy leg.). However, *A. boucheti* differs from this latter species by its smaller size (*A. guttata* can reach 5.0 mm width), by a much thicker and heavier shell, a coloration pattern of radiating grayish-green flamules instead of the random dotting of pink present in *A. guttata.* The spiral sculpture in *A. boucheti* consists of cords with rounded nodules; beading on the cords of *A. guttata* results from the overlapping of 5 to 8 layers of prosocline lamellae. There are 24–32 nodules on the final whorl in *A. boucheti,* and about 45 in *A. guttata.* The aperture in *A. boucheti* is characterized by a deep embayment in the columellar region and parietal wall. This embayment extends to the umbilicus. The aperture is holostomatous in *A. guttata,* without indentation. Strong teeth are present inside the outer lip in *A. boucheti,* while only faint denticles are found in *A. guttata.*

Other species probably related to *A. boucheti* and *A. lurida* (Dall 1913), from the coast of Baja California, Mexico, and '*Cinysca*' *pacifica* Ladd, 1966, from the Miocene of Eniwetok Atoll. '*Cinysca*' *pacifica* is known to me only from the illustration in the original description (Ladd 1966). A comparison of the type series of *A. boucheti* with shells of *A. lurida* (LACM 66-28.2, 20 shells, Bahia Partida [between Islas Partida and Espíritu Santo], Gulf Coast, Baja California Sur, Mexico [24°31'N, 110°23'W], coll. McLean, Oringer and Marincovich, 10 Apr 1966) shows that the latter species has more angulose whorl profiles, dark red color, and more delicate, less distinctive nodules in the shell surface.

Acknowledgments

I thank P. Bouchet (MNHN) for providing the resources for field work in Trindade Island in 1987 and for criticizing an earlier version of this paper. A. Guille and J. M. Ramos were chief-scientists during the cruise MD55 of the *Marion-Dufresne.* J. H. McLean (LACM) presented unpublished information on the supraspecific relationships among the turbinids, loaned material of *Arene* from the eastern Pacific, and reviewed the manuscript. P. L. Blackwelder placed at my disposal the SEM at the Electron Microscope Laboratory, RSMAS, University of Miami. N. B. Barros helped with proofreading. Funding was provided in part by a doctoral scholarship from Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil. Additional support was given by the Naples, Sanibel-Captiva, Astronaut Trail, and National Capital Shell Clubs, Conchologists of America, Bader Memorial Student Research Fund, Rowlands Fellowships, and Reitmeister Fellowship for Conservation Studies.

Literature Cited

Abbott, R. T. 1974. American seashells. Second Edition. Van Nostrand-Reinhold, New York, 663 pp.

Barnard, K. H. 1963. Contributions to the knowledge of South African marine Mollusca. Part 4. Gastropoda, Prosobranchiata: Rhipidoglossa, Docoglossa. Tectibranchiata. Polyplacophora. Solenogastres. Scaphopoda.—Annals of the South African Museum 47:201–360.

Dall, W. H. 1913. Diagnoses of new shells from the Pacific Ocean.—Proceedings of the United States National Museum 45(2002):587–597.

Diretoria de Hidrografia e Navegação. 1985. Brasil–Ilhas ao Largo–Trindade e Martin Vaz. Carta Náutica no. 21. [reproduced in U.S. Defense Mapping Agency/Topographic Center, Islands off Brazil–Ilhas da Trindade and Martin Vaz. Chart no. 24451].

Hickman, C. S. 1984. Implications of radular tooth-

row functional integration for archaeogastropod systematics.—Malacologia 25:143–160.

———, & J. H. McLean. 1990. Systematic revision and suprageneric classification of trochacean gastropods. Natural History Museum of Los Angeles County Science Series 35, 169 pp.

Kilburn, R. 1970. Taxonomic notes on South African marine Mollusca, 1.—Annals of the Cape Provincial Museum 8(4):39–48.

Ladd, H. S. 1966. Chitons and Gastropoda (Haliotidae through Adeorbidae) from the western Pacific islands.—Geological Survey Professional Paper 531: 98 pp.

Leal, J. H., & A. C. S. Coelho. 1985. *Arene flexispina,* a new species (Gastropoda: Liotiidae) from off eastern Brazil.—The Nautilus 99(2–3):45–47.

———, & P. Bouchet. 1991. Distribution patterns and dispersal of prosobranch gastropods along a seamount chain in the Atlantic Ocean.—Journal of the Marine Biological Association of the United Kingdom 71(1): 11–25.

Marshall, B. A. 1988. Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales.—Journal of Natural History 22:949–1004.

McLean, J. H. 1970a. New species of Panamic marine gastropods.—The Veliger 12(3):310–315.

———. 1970b. New species of tropical eastern Pacific Gastropoda.—Malacological Review 2:115–130.

———. 1971. Order Archaeogastropoda. Pp. 307–362 *in* A. M. Keen, Seashells of tropical west America—Marine mollusks from Baja California to Peru. Second Edition. Stanford University Press, Stanford.

———. 1987. Angariinae and Liotiinae—the primitive living trochaceans.—Annual Report of the Western Society of Malacologists 19:16.

———, R. S. Absalão, & R. L. S. Cruz. 1988. A new species of Macrarene (Turbinidae: Liotiinae) from Brazil.—The Nautilus 102(3):99–101.

Morgan, W. J. 1983. Hotspot tracks and the early rifting of the Atlantic.—Tectonophysics 94:123–139.

Mühlfeld, M. von. 1829. Fortsetzung von John Cave Megerle von Mühlfeld's Beschreibung einiger neuen Conchylien.—Verhandlungen der Gesselschaft Naturforschender Freunde zu Berlin 1(4):205–221.

Olsson, A. A., & A. Harbison. 1953. Pliocene Mollusca of southern Florida, with special reference to those from North Saint Petersburg with special chapters on Turridae by William G. Fargo and Vitrinellidae and fresh-water mollusks by Henry A. Pilsbry.—Monographs of the Academy of Natural Sciences of Philadelphia 8:1–457.

Pilsbry, H. A. 1888. Monographs of the Turbinidae and Trochidae. Pp. 161–323 *in* G. W. Tryon, Jr. & H. A. Pilsbry, eds., Manual of conchology. Volume 10, Part 2. Philadelphia, 323 pp.

Rios, E. C. 1985. Seashells of Brazil. Fundação Universidade do Rio Grande, Rio Grande, 328 pp.

Stearns, R. E. C. 1872. Description of new species of marine mollusks from the coast of Florida.—Proceedings of the Boston Society of Natural History 15:21–24.

Division of Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149-1098.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 247–252

ANNINA FUSTIS, A NEW ISOPOD FROM PHANG NGA, THAILAND (CRUSTACEA: ISOPODA: CIROLANIDAE)

Thomas E. Bowman and Thomas M. Iliffe

Abstract.—*Annina fustis,* the fourth known species of *Annina,* is described from a remnant limestone cave near Phang Nga, in peninsular Thailand. It is distinguished by the rounded frontal lamina, and in the male by the long club-shaped horns on pereonite 2 and the fusion of flagellar segments 1 and 2 of antenna 2.

Annina Budde-Lund, 1908, is a small genus of 3 species known from springs, ponds, and subterranean lakes, and from mangrove swamps, from burrows either in the mud or in mangrove stumps. The genus is close to *Excirolana* Richardson, 1912, from which it differs in having a non-facetted gap separating dorsal and ventral parts of the eye, in pleonites 1–2 being narrower than pleonites 3–5, and especially in two characters found only in the male: the presence of dorsal horns on pereonite 2 and sometimes also on the head and pereonite 1; the modified antenna 2. A revised diagnosis of *Annina* with a key to the 3 species is given by Jones (1983).

We describe herein a fourth species from Thailand.

Cirolanidae Dana, 1853
Annina Budde-Lund, 1908
Annina fustis, new species
Figs. 1–3

Material.—Thailand, Phang Nga (8°30′N, 98°30′E), Tum Rusee ("Tum" = "cave" in Thai), Iliffe Station 85-094, muddy bottom of stream and pools, depths 0–30 cm, collected with small dip net by Thomas M. Iliffe and Yolanda Iliffe, 4 May 1985, holotype ♂ 7.0 mm, USNM 250558; paratypes, 8 ♀, 4.4–7.0 mm, 8 ♂, 4.4–6.3 mm, USNM 250559.

Comparative material.—*Annina mesopotamica* (Ahmed): Iraq, near Basrah, from stream Shatt-Al-Arab, leg. M.M. Ahmed, 19 Sep 1972, 7 ♂ ♀, USNM 213137.

Description.—Length up to 7.0 mm, about 4× as long as wide, greatest width at pereonite 5. Head with slightly concave dorsum lacking processes. Pereonite 1 without processes. Pereonite 2 of ♂ with dorsal horns reaching to about anterior 4th of pereonite 1; horns tapering to point in dorsal view, in lateral view expanding apically into rounded tip produced further ventrally than dorsally; minute tubercle sometimes present at midwidth of anterior margin. Pereonite 2 of ♀ without horns.

Pleotelson about 5/6 as long as wide, triangular, apex narrowly rounded. Posterior half of each lateral margin with about 12 notches, each notch bearing a seta. Apex with several submarginal long setae; dorsum with scattered short setae.

Frontal lamina broadly rounded anteriorly, not fused with triangular rostrum. Clypeus produced into acute process (in lateral view).

Antenna 1 reaching slightly posterior to anterior margin of pereonite 3; peduncle segment 3 slightly shorter than combined lengths of peduncle segments 1 and 2; flagellum about 14-segmented, segments 1–3 without esthetes, other segments with 1 or 2 esthetes. Antenna 2 of ♀ reaching pereonite 6; peduncle 5-segmented, segment 1 (Fig. 1G) closely adhering to head and usually

not freed in dissection, segment 5 about as long as segments 3 and 4 combined; flagellum about 11-segmented. Antenna 2 of ♂ with distinctly broader peduncle segments, peduncle segment 5 longer than segments 2–4 combined; segments 1 and 2 of flagellum fused, with expanded posterodistal corner; segment 3 also with expanded posterodistal corner.

Mandible lacinia with 10 teeth; palp segment 2 with 2 long setae at midlength and subapically on medial margin. Maxilla 1 exopod with 12 strong marginal spines and 1 slender spine inserted in gnathal surface. Maxilla 2 with 7 and 9 setae on palp and exopod respectively, exopod with 11 setae and numerous hairs.

Maxilliped (Fig. 3B, C) and pereopods (Fig. 2A–G) typical for the genus *Annina*. Appendix masculina tapering to smooth point, not quite reaching distal margin of pleopod 2 endopod. Uropod very similar to that of *A. kumari* (Bowman 1971); protopod short, distomedial corner strongly produced; endopod subpyriform, about 2.4× as long as wide, both margins with notches bearing plumose setae; exopod lanceolate, shorter and much narrower than endopod, only medial margin notched and bearing plumose setae.

Etymology.—From the Latin noun "fustis," a club, referring to the flattened club-shape of the horns of pereonite 2 when viewed laterally.

Sexual dimorphism.—In the Cirolanidae, sexual dimorphism, aside from the presence of oostegites in females and penes and appendix masculina in males, is usually absent or only slightly developed. Sexual differences may occur in body proportions (♂ more elongate), in cuticular ornamentation (more prominent in ♂), and in the structure of pereopod 1 and the uropods. The striking difference in antenna 2, found in all species of *Annina,* is quite unusual. Furthermore, in 2 of the species, *A. kumari* and *A. fustis,* flagellar segments 1 and 2 of antenna 2 are fused in the fully differentiated ♂, whereas in the other 2 species, *A. lacustris* Budde-Lund, 1908, and *A. mesopotamica* (Ahmed 1971), ♂ flagellar segments 1 and 2 remain separate. Fusion of these segments is apomorphic, since in juvenile males as in females of *A. fustis* these segments are distinct (Fig. 1J). Sexual dimorphism of antenna 2 is found also in *Limicolana dinjerra* Bruce (1986), in which the distal segment of the peduncle is swollen in the ♂ but not in the ♀.

Comparison.—The 3 previously known species of *Annina* may be distinguished from *A. fustis* by the following:

A. lacustris (East Africa; Zanzibar (Budde-Lund 1908; Monod 1968); Gazi Bay, Kenya (Jones & Icely 1981, as *E. bowmani*); Comoro Islands (Messana 1984)).

—dorsum of ♂ head, pereon, and pleon with numerous tubercles.
—horns of pereonite 2 in lateral view sinuate, not expanding at apex which is produced further dorsally than ventrally.
—telson and endopod of uropod apically truncate.
—♂ antenna 2 flagellar segments 1 and 2 distinct.

A. kumari (Port Swettenham, Malaysia (Bowman 1971)).

—♂ with pair of horns on head, pereonite 1, and pereonite 2, those on pereonite 2 very short and apically acute.
—apex of frontal lamina pointed in dorsal view.

A. mesopotamica (near Basrah, Iraq (Ahmed 1971)).

—horns of ♂ pereonite 2 very short, blunt (Fig. 1N).
—♂ antenna 2 flagellar segments 1 and 2 distinct.

Habitat.—The town of Phang Nga is located at 8°30′N, 98°30′E on the northern end of Phang Nga Bay, an estuary on the Andaman Sea in southern Thailand. Between the town and the bay is an extensive area of limestone tower karst situated on a mangrove-forested river flood plain. Tum Rusee is located in a park just east of Phang Nga at the edge of this mangrove forest. It is an inland eroded remnant cave consisting

Fig. 1. A–M, *Annina fustis*: A, ♂ habitus, dorsal; B, ♂ pereon, lateral; C, ♂ head and pereonites 1–2, dorsal; D, ♀ head and pereonites 1–2, lateral; E, ♂ pereonites 1–2, lateral; F, Right eye, lateral; G, Buccal area, ventral; H, ♂ left antenna 1, dorsal; I, ♂ left antenna 2, dorsal; J, Left antenna 2, dorsal, 4.4 mm ♂; K, ♀ left antenna 2, dorsal; L, Maxilla 1; M, Maxilla 2. N–O, *Annina mesopotamica*: N, ♂ pereonites 1–2, lateral; O, ♂ left antenna 2, dorsal. (Segment 1 of peduncle not shown in I and O).

Fig. 2. *Annina fustis* ♂: A–G, Pereopods 1–7; H, Uropod, dorsal; I, Pleotelson, dorsal.

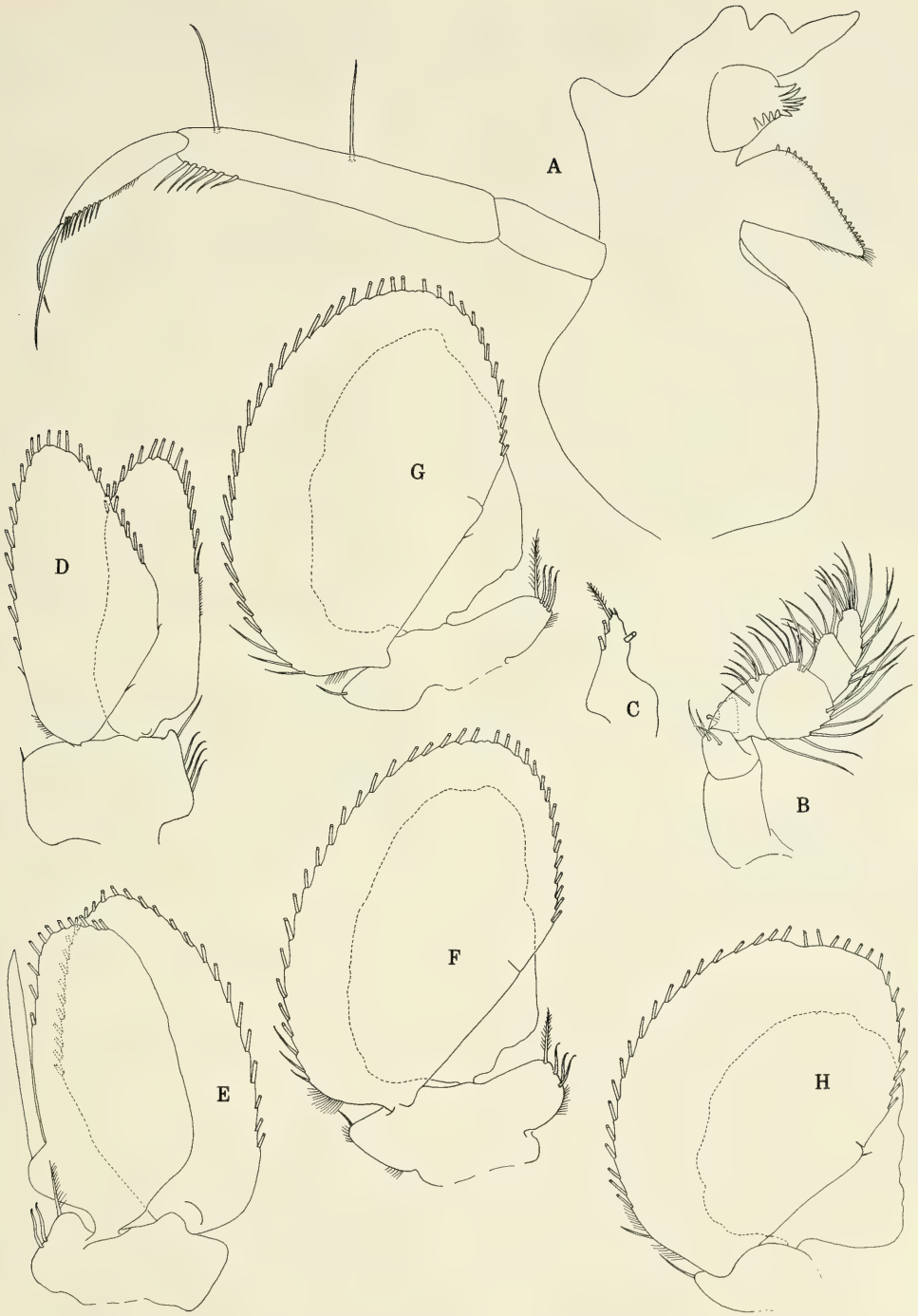


Fig. 3. *Annina fustis* ♂: A, Left mandible; B, Maxilliped; C, Endite of maxilliped; D–H, Pleopods 1–5.

of a small shallow stream flowing through natural archways. In addition to the *Annina fustis,* shrimps and crabs still under study were collected from the Tum Rusee stream. Dr. Niel L. Bruce (in litt. 17 Oct 1990) has generously suggested that I mention here his 2 samples of what is almost certainly *Annina fustis* from mangroves in Singapore.

Acknowledgments

Collection of specimens from caves in the Indopacific was supported by a grant from the National Science Foundation (BSR 8417494) to Thomas M. Iliffe. We thank the Phuket Marine Biological Center for providing logistical information on Phang Nga and Yolanda Iliffe for assistance in collecting from the caves.

Literature Cited

Ahmed, M. M. 1971. New Isopoda (Flabellifera) from Iraq and Arabian Gulf.—Mitteilungen aus dem Zoologischen Museum in Berlin 43(1):77–83.

Bowman, T. E. 1971. *Excirolana kumari,* a new tubicolous isopod from Malaysia.—Crustaceana 20:70–76.

Bruce, N. L. 1986. Cirolanidae (Crustacea: Isopoda) of Australia.—Records of the Australian Museum, Supplement 6:1–239.

Budde-Lund, G. 1908. Isopoda von Madagaskar und Ostafrika mit Diagnosen verwandter Arten, *in* A. Voeltzkow, Reise in Ostafrika in dem Jahren 1903–1905, Wissenschaftliche Ergebnisse 2:265–308, pls. 12–18.

Dana, J. D. 1853. Crustacea, Part 2.—United States Exploring Expedition 14:689–1618.

Jones, D. A. 1983. On the status of the cirolanid isopod genera *Annina* Budde-Lund, 1908 and *Excirolana* Richardson, 1912.—Crustaceana 45(3):309–312.

———, & J. D. Icely. 1981. *Excirolana bowmani,* a new mangrove-boring isopod from Kenya (Isopoda, Cirolanidae).—Crustaceana 40(3):266–271.

Messana, G. 1984. A new locality for *Annina lacustris* Budde-Lund, 1908. Some considerations on taxonomy and reproduction of the genera *Annina* and *Excirolana* (Isopoda, Cirolanidae).—Revue de Zoologie Africaine 98:766–770.

Monod, T. 1968. Isopoda. Pp. 498–507 *in* I. Gordon & T. Monod, Sur quelques Crustacés des eaux douces de Zanzibar.—Bulletin de l'Institut Français d'Afrique Noire 30A(2):497–517.

Richardson, H. 1912. Descriptions of a new genus of isopod crustaceans, and of two new species from South America.—Proceedings of the United States National Museum 43(1929):201–204.

(TEB) Department of Invertebrate Zoology (Crustacea), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (TMI) Department of Marine Biology, Mitchell Campus, P.O. Box 1675, Texas A&M University at Galveston, Galveston, Texas 77553.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 253–268

REVISION OF IPHIMEDIIDAE AND SIMILAR FAMILIES (AMPHIPODA: GAMMARIDEA)

C. O. Coleman and J. L. Barnard

Abstract.—The amphipod families Acanthonotozomatidae, Amathillopsidae, Astryidae, Epimeriidae (=Paramphithoidae), Iphimediidae, Ochlesidae and Stilipedidae are rediagnosed and three new families, Acanthonotozomellidae, Dikwidae, and Odiidae are described. New keys distinguish these families; other similar families, Lafystiidae and Laphystiopsidae are diagnosed and included in the keys.

In the process of rediagnosing the Ochlesidae Stebbing, 1910 (see Coleman & Barnard 1991a), as a family distinct from Iphimediidae, we determined that other alterations to the taxonomy of the Iphimediidae and Epimeriidae were necessary. Our contribution here offers a different division than used in the past based on characters not previously used or inconsistently used to define these groups. For example, we found relatively good consistency of characters on incisors, rakers, gnathopods and coxae in proposing this new division of the taxa.

Discussion

By using characters other than reduction of maxillipedal palp, we are able to tighten the diagnosis of Ochlesidae, but this requires, at the same time, the removal of the genera *Odius* and *Postodius* from the Iphimediidae to form the contents of a new family Odiidae, the removal of the peculiar *Dikwa* from its paramphithoid-iphimediid associations to form a unique family Dikwidae, and the reinstatement of the Amathillopsidae (an old family synonymized with Epimeriidae some years ago). The genera *Parepimeria* Chevreux (1911) and *Parepimeriella* Schellenberg (1931) are removed to the Pleustidae. By removing the above contents from the two families, the diagnosis of Epimeriidae becomes strengthened and these amphipods can be distinguished more discretely from Iphimediidae, without resorting to the difficult judgment about the conical or quadrate shapes of the mouthpart group. Within the Iphimediidae two principal groups remain: those genera similar to *Iphimedia* and those genera similar to *Acanthonotozoma.* These two groups are distinguished and the Acanthonotozomatidae are revived. The new family Acanthonotozomellidae are split away from Acanthonotozomatidae.

Methods

All diagnoses presented herein follow the format of comparison to the model amphipod known as the "basic gammaridean" published by Barnard (1969:50, figs. 1, 2). The formula for setae on the mandibular palp was invented by Stock (1974). Two keys with different starting points are presented. To account for possible differing interpretations of certain characters some taxa are entered twice in the keys. For example, Dikwidae are entered twice to treat the alternatives of coxa 1 acuminate and tapering, or subtruncate and not tapering.

Key I to the Families of the Iphimediidae and Similar Taxa

1. Mandibular rakers present 2
– Mandibular rakers absent 10
2. Coxa 1 truncate, not pointed or tapering 3

– Coxa 1 tapering or pointed 7
3. Gnathopod 1 propodochelate, head deformed ..... Dikwidae
– Gnathopod 1 not propodochelate 4
4. Molar triturative ... Amathillopsidae
– Molar not triturative, or absent .. 5
5. Neither molar present nor incisor broadened .. Acanthonotozomellidae
– Either molar present or incisor broadened 6
6. Small setose molar present, incisors narrow ..... Astryidae
– Molar absent, incisors very broad ..... certain Stilipedidae
7. Gnathopod 2 much broader than gnathopod 1, carpus lobate .. Odiidae
– Gnathopod 2 almost as slender as gnathopod 1, carpus not lobate .. 8
8. Gnathopod 1 propodochelate, head deformed and reduced .... Dikwidae
– Gnathopod 1 simple, head formed normally 9
9. Molar absent .... Acanthonotozomellidae
– Molar present ..... Epimeriidae
10. Coxa 1 truncate below 11
– Coxa 1 tapering below 14
11. Gnathopods 1–2 propodochelate ..... Iphimediidae
– Gnathopods 1–2 not propodochelate 12
12. Body and incisors of mandible very broad and flat ..... Stilipedidae
– Body and incisors of mandible ordinary 13
13. Gnathopod 2 subchelate, molar absent, coxa 4 not reduced, pointed ..... Lafystiidae
– Gnathopod 2 simple, molar present, all coxae 1–4 reduced, truncate ..... Laphystiopsidae
14. Gnathopod 2 propodochelate ... . Iphimediidae
– Gnathopod 2 not propodochelate 15
15. Carpus of gnathopod 2 produced, molar present ..... Ochlesidae
– Carpus of gnathopod 2 not produced, molar absent .... Acanthonotozomatidae

Key 2 to the Families of the Iphimediidae and Similar Taxa

1. Gnathopod 1 propodochelate 2
– Gnathopod 1 subchelate or simple 4
2. Gnathopod 2 enlarged, subchelate, carpus lobate, (molar triturative, rakers present) ..... Odiidae
– Gnathopod 2 feeble, propodochelate or simple, carpus not lobate 3
3. Rakers present, gnathopod 2 simple ..... Dikwidae
– Rakers absent, gnathopod 2 propodochelate ..... Iphimediidae
4. Carpus of gnathopod 2 produced ..... Ochlesidae
– Carpus of gnathopod 2 not produced 5
5. Coxa 1 tapering or pointed 6
– Coxa 1 not tapering or pointed .. 8
6. Molar produced, triturative or setose ..... Epimeriidae
– Molar reduced or absent, not triturative or setose 7
7. Rakers absent .... Acanthonotozomatidae
– Rakers present .... Acanthonotozomellidae
8. Incisors extremely broad and flat ..... Stilipedidae
– Incisors of ordinary width and not extremely flat 9
9. Rakers present 10
– Rakers absent 11
10. Molar only setose, gnathopods feeble, propodus smaller than carpus, rectangular or ovate ..... Astryidae
– Molar triturative, gnathopods enlarged, propodus larger than carpus, almost almond-shaped .... Amathillopsidae
– Molar absent, gnathopods feeble, propodus dominated by carpus, subrectangular .... Acanthonotozomellidae

11. Gnathopod 2 subchelate, molar absent, coxa 4 not reduced, tapering ..... Lafystiidae
– Gnathopod 2 simple, molar present, all coxae 1–4 reduced, truncate ..... Laphystiopsidae

Special Couplets Distinguishing Ochlesidae and Odiidae

A. Pereonites 1–6 flat and keel-like dorsally, flagella of both antennae 1–2 reduced, merus and carpus of gnathopod 2 produced, palp of maxilla 1 reduced, inner plate of maxilla 1 reduced ..... B
B. Gnathopod 1 simple, gnathopod 2 simple, coxae 1 and 4 shorter than coxae 2–3 ..... Ochlesidae
– Gnathopod 1 propodochelate, gnathopod 2 subchelate, coxae 1 and 4 ordinary ..... Odiidae

Amathillopsidae

Amathillopsidae Pirlot, 1934:201.

Diagnosis.—Body compressed. Rostrum of medium size or very small (not "well developed"). Antennae elongate, flagella with 5+ articles; accessory flagellum 1–2 articulate. Mouthpart part field quadrately developed (box-like). Epistome and labrum broad, short, entire. Incisor of mandible ordinary, toothed; raker row strong; molar large and triturative, palp always present, 3-articulate. Lower lip with large fleshy inner lobes, without distinct inner notches. Inner plate of maxilla 1 ordinary, apically and somewhat medially setose; outer plate oblique, normally spinose; palp large, 2-articulate. Inner plate of maxilla 2 without facial setae. Palp of maxilliped 4-articulate, article 2 not produced medially. Coxae 2–3 more or less acuminate, ventral margins fitting normal ventral parabolic curve of anterior coxae; coxa 1 but not 4 shortened, coxa 1 scarcely to not acuminate, mostly truncate, coxa 4 not strictly acuminate, with weak or no posteroventral lobe, coxa 5 at least slightly shorter than 4. Gnathopods of moderate size and with short articles 5–6, not flagellar, gnathopod 2 usually slightly longer than gnathopod 1; gnathopods 1–2 propodosubchelate, carpi lobed, propodi enlarged and almost almond-shaped. Article 2 of pereopods 5–7 occasionally with posterior cusps or teeth. Epimeron 3 lacking 2 large cusps. Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 flattened, lanceolate, 1-articulate. Telson entire or weakly incised, generally not longer than peduncle of uropod 3.

Relationship.—Differing from the Epimeriidae in the weaker rostrum, slightly shortened and unpointed coxa 1, lobate carpi and enlarged almond-shaped propodi of gnathopods, and presence of large inner lobes on the lower lip.

List of genera.—*Amathillopsis* Heller, 1875 (=*Acanthopleustes* Holmes, 1908).

Epimeriidae

Epimerinae [sic] Boeck, 1871:183.
Paramphithoidae Stebbing, 1906:320.

Diagnosis.—Body compressed, with dorsal teeth sometimes confined to metasome, or urosome, and sometimes weak (*Epimeriella*). Rostrum well developed. Antennae elongate, flagella with 5+ articles; accessory flagellum 0–1 articulate. Mouthpart part field quadrately developed (box-like). Epistome and labrum broad, short, incised or entire. Incisor of mandible ordinary, toothed; raker row strong; molar large and triturative or reduced, conical and pubescent (*Epimeriella* and *Epimeria victoria* Hurley, 1957); palp always present, 3-articulate. Lower lip without inner lobes, without distinct inner notches. Inner plate of maxilla 1 ordinary, medially setose (except *Uschakoviella*); outer plate oblique, normally spinose; palp large, 2-articulate. Inner plate of maxilla 2 without facial setae. Palp of maxilliped 3–4-articulate, article 2 not produced medially. Coxae 1–4 acuminate, ventral margins fitting normal ventral parabolic curve of anterior coxae; coxae 1 and

4 not shortened, coxa 4 with large posteroventral lobe, coxa 5 at least slightly shorter than 4. Gnathopods feeble and with elongate articles 5–6 but not flagellar, gnathopod 2 usually slightly longer than gnathopod 1; gnathopods 1–2 propodosubchelate, or simple, merus and carpus not produced. Article 2 of pereopods 5–7 often with posterior cusps or teeth. Epimeron 3 lacking 2 large cusps (though occasional species with very small epimeral bicuspidation), occasionally body or coxae with surficial cusps or rarely articulate spines (*Uschakoviella*). Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 longer than peduncle, flattened, lanceolate, usually 1-articulate. Telson entire or weakly incised, generally not longer than peduncle of uropod 3.

Relationship.—Differing from the Acanthonotozomatidae in the box-like field of mouthparts and the well developed mandibular molar and the non-flagellar gnathopod 1.

Differing from the Odiidae in the well developed flagella of antenna 1, well developed medial setae on the first maxillae, absence of distinct medial notches on the main lobes of the lower lip, strongly acuminate coxae 1–3, and well developed (versus reduced) D–E setae on the mandibular palp (an accessory character not otherwise used in diagnoses).

The maxillipedal palp of Ochlesidae is 0–2 articulate, coxa 4 is shortened, the merus and carpus of gnathopod 2 is otherwise produced, and the pereon has an anterior keel, except *Meraldia* which has a series of dorsal plaques.

Differing from the Acanthonotozomellidae in the presence of a molar.

The Iphimediidae have chelate gnathopods and have a severely reduced molar.

The Dikwidae have a chelate gnathopod 1, flagellar gnathopod 2, and reduced head.

The Pardaliscidae have poorly developed inner plates on the maxillipeds and one of the mandibles is heavily flattened; usually pardaliscids have an elongate accessory flagellum. Most Pardaliscidae have evenly extending coxae 1–7, there being little difference in the ventral extension of these plates.

The Stilipedidae have an expanded, nonacuminate coxa 1, and foliaceous mandibles. The Astryidae have a lower lip with widely separated outer lobes and the gnathopods have a characteristic pattern, the carpus being weakly lobate but much wider than the thinner, simple propodus. The Stilipedidae have an exaggerated version of this kind of gnathopod but the carpus is not so strongly lobate as it is strongly enlarged.

Stegocephalidae lack a mandibular palp.

Dexaminidae have fusion of certain urosomites and normal maxillipeds.

Pleustidae have characteristic lower lips.

Gammaridans with acuminate coxae have a large accessory flagellum and normal maxillipeds.

Within Pontoporeiidae *Priscillina* also bears acuminate coxae but differs otherwise from Epimeriidae in the multiarticulate accessory flagellum and short inner ramus of uropod 3 (gammaroid facies).

Rhachotropis is distinguished from Epimeriidae (except *Epimeria yaquinae*) in the large gnathopods with expanded propodus and short deeply lobate carpus; the telson is elongate. *Oradarea* in the Eusiridae has an occasional species with incipiently acuminate coxae. *Cleippides quadricuspis* has points on some anterior coxae, but no coxa tapers to a single point downward.

Amathillopsidae appear similar to eusirid-calliopiid groups, but differ in the short telson. The ratio of size between the plates and the palps of the maxilliped in Amathillopsidae are not typical for Epimeriidae (a character not otherwise used in the diagnoses). The shape of the gnathopods differs strongly from all Epimeriidae.

Removals.—*Parepimeria* Chevreux (1911) and *Parepimeriella* Schellenberg (1931) are removed to the Pleustidae because of the condition of lower lips and maxillipeds.

Eclysis and *Epimeriella* were removed to

the Astryidae by Andres (1985). Walker (1907) originally differentiated *Epimeriella* from *Epimeria* on the lack of significant dorsal body cuspidation, lack of a point on coxa 5, the elongate pereopods 5–6, smallness of rostrum, and the imperfect molar. His two figures of coxa 1 on his plate 9 are slightly different views but show some tapering. Gnathopod 1 is less typical of Astryidae than of Epimeriidae. Andres (1985) partially described some non-type specimens of the type species. *Epimeriella macronyx,* but no full analysis and figures of a single specimen, nor comparison with types appears to be present in the literature. Gnathopods have not been reillustrated. Andres addresses dactylar lengths of pereopod 5 but not overall lengths relative to pereopod 7. Coxae 1–2 of the type species are not illustrated but coxae 1–2 of *Epimeriella truncata* show coxa 1 definitely blunt distally but not as greatly and disproportionately widened as in species of *Astrya* and *Stilipes.* The gnathopodal carpi are much less dominant than in species of *Astrya* and *Stilipes,* and scarcely differ from the classic *Epimeria cornigera* shown by Sars (1895:pl. 128).

Epimeriella victoria (Hurley 1957; and see Moore 1985) has a narrow pointed coxa 1, unlike other supposed members of the genus (but coxa 1 of the type-species of *Epimeriella* is still not well documented). The close congruency of mandibular molar of *E. victoria* to the other species of *Epimeriella* suggests there might be a close relationship; one may establish a transformation series between the least cuspidate species of *Epimeriella* and *E. victoria* to account for the very cuspidate conditions in the latter. For the moment we have removed *E. victoria* to *Epimeria.* It fits into Epimeriidae as well as it does into Astryidae; it differs from Astryidae in its tapering coxa 1 and from Epimeriidae in the reduced molar and slightly more opened outer lobes of the lower lip. It fits Epimeriidae better because of the cuspidation character of its body and coxae and the weakness of carpal expansion on the gnathopods. The latter character is a problem of context and needs much better documentation in the literature than heretofore available.

List of genera.—*Paramphithoe* Bruzelius, 1859 (=*Acanthosoma* Ross, 1835, homonym, Hemiptera) (=type genus); *Actinacanthus* Stebbing, 1888; *Epimeria* Costa, 1851, 1851–1853 (=*Pseudepimeria* Chevreux, 1912a, 1912b, =*Subepimeria* Bellan-Santini, 1972); *Epimeriella* Walker, 1906, 1907; *Metepimeria* Schellenberg, 1931; *Uschakoviella* Gurjanova, 1955.

Acanthonotozomellidae, new family

Type genus.—*Acanthonotozomella* Schellenberg, 1926.

Diagnosis.—Body compressed, with dorsal teeth (except *Acanthonotozomopsis*). Rostrum well developed (except *Acanthonotozomopsis*). Antennae elongate or short, flagella with 5+ articles, rarely with 2 (*Amatiquakius*); accessory flagellum absent. Mouthpart part field conical. Epistome and labrum narrow, long, incised. Incisor of mandible ordinary, toothed; raker row strong; molar reduced or absent; palp always present, 3-articulate. Lower lip without inner lobes, without distinct inner notches. Inner plate of maxilla 1 ordinary, medially setose or setation reduced; outer plate oblique, normally spinose; palp large, 2-articulate. Inner plate of maxilla 2 without facial or medial setae. Palp of maxilliped 4-articulate, article 2 often produced medially. Coxae 2–4 more or less acuminate, ventral margins fitting normal ventral parabolic curve of anterior coxae or in type genus coxa 2 shortened; coxae 1 and 4 not shortened, coxa 1 widened in 2 genera but not significantly wider than coxa 2 (versus Stilipedidae), subtruncate or rounded (except *Acanthonotozomoides* with concave margin and anteroventral tooth), coxa 4 with large posteroventral lobe (except *Acanthonotozomopsis* and small in *Amatiquakius*).

Coxa 5 shorter than posteroventral lobe of 4. Gnathopods feeble, subequal; gnathopods 1–2 simple or weakly parachelate, merus and carpus not produced, carpi slender. Article 2 of pereopods 5–7 often with posterior cusps or teeth. Epimeron 3 often with 2 large cusps posteroventrally. Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 longer than peduncle, flattened, lanceolate, 1-articulate. Telson entire or weakly incised, generally not longer than peduncle of uropod 3.

Relationship.—See the Epimeriidae, Odiidae, Ochlesidae, for distinctions from those families and see Epimeriidae for mention of families outside of the iphimedioid group of families included herein, which differ in the same way as from Acanthonotozomellidae.

Differing from the Acanthonotozomatidae in the presence of rakers on the mandible.

Differing from the Iphimediidae in the presence of rakers, the simple gnathopods 1–2, and in the absence of medial setae on the inner plate of maxilla 2.

Differing from the Dikwidae in the absence of a molar, the normal head, simple gnathopod 1, and the non-flagellar gnathopod 2.

Acanthonotozomella and *Acanthonotozomopsis* share with Stilipedidae a slightly expanded coxa 1, and in most species coxae 1–3 are not sharply pointed but rather truncate or rounded. The Stilipedidae are distinguished by the immensely broadened mandibles.

The mandibular incisors in Acanthonotozomellidae move plesiomorphically in the "horizontal transverse plane of the body and in a plane perpendicular to the long axis of the mandible" (Watling & Thurston 1989), whereas in the Iphimediidae there occurs gradual change of the cutting plane towards the "vertical frontal plane of the body and in the medial-lateral plane through the long axis of the mandible." This transition of the cutting plane, however, cannot be used to separate Acanthonotozomellidae from Iphimediidae, because *Pseudiphimediella* bears the plesiomorphic mandibular conditions.

Maxilliphimedia bears the fully plesiomorphic mandibular conditions and *Anchiphimedia* intermediates between the plesiomorphic state and the apomorphic frontal mandibular cutting plane (compare with Watling & Thurston 1989). These two genera differ from Stilipedidae in the chelate gnathopods with otherwise completely different form than in Stilipedidae and in the paired dorsal cusps typical of most iphimediids.

Acanthonotozomellidae are similar to Stilipedidae and Astryidae in that coxa 1 is expanded and apically truncate or rounded in most species of Acanthonotozomellidae. For the most part coxa 1 of Acanthonotozomellidae is not broader than coxa 2 as in Astryidae and Stilipedidae. Astryidae have a molar and Stilipedidae have broadened mandibular bodies and incisors. The gnathopods of Acanthonotozomellidae are subtly distinct from those of Astryidae and Stilipedidae where the carpus significantly dominates the propodus in its breadth.

Composition.—*Acanthonotozomella* Schellenberg, 1926 (=*Paracanthonotozoma* Bellan-Santini, 1972); *Acantonotozomoides* Schellenberg, 1931; *Acanthonotozomopsis* Watling & Holman, 1980; *Amatiquakius* Coleman & Barnard, 1991b.

Acanthonotozomatidae Stebbing

Acanthonotozomatidae Stebbing, 1906:210.

Diagnosis.—Body compressed, with or without dorsal teeth. Rostrum well developed. Antennae elongate, flagella with 5+ articles; uniarticulate accessory flagellum present. Mouthpart field conical. Epistome and labrum narrow, long, incised. Incisor of mandible narrow, toothed; raker row absent; molar reduced or absent; palp always present, 3-articulate. Lower lip apically pointed, without inner lobes, without dis-

tinct inner notches. Inner plate of maxilla 1 ordinary, medially setose; outer plate oblique, normally spinose; palp large (somewhat shortened in *A. cristatum*), 2-articulate. Inner plate of maxilla 2 without facial setae. Palp of maxilliped 4-articulate, article 2 not produced medially. Coxae 1–4 acuminate, ventral margins fitting even curve or straight line of anterior coxae; coxae 1 and 4 not shortened, coxa 4 with large posteroventral lobe, coxa 5 slightly shorter than 4. Gnathopod 1 feeble, slender, articles 5–6 weakly elongate, gnathopods 1–2 propodosubchelate, merus and carpus not produced. Article 2 of pereopods 5–7 often with posterior cusps or teeth. Epimeron 3 with 2 large cusps posteromarginally (except *Acanthonotozoma cristatum*), occasionally body or coxae with surficial cusps. Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 longer than peduncle, flattened, lanceolate, 1-articulate. Telson weakly incised, generally not longer than peduncle of uropod 3.

Relationship.—The Epimeriidae differ in the well developed mandibular molar. See Epimeriidae for mention of differences from families outside of the families included herein.

See the Odiidae, Ochlesidae, Acanthonotozomellidae, Iphimediidae, and the Dikwidae for distinctions from those families.

List of genera.—*Acanthonotozoma* Boeck, 1876 (=*Acanthonotus* Ross, 1835 [=homonym, Pisces], =*Panoploeopsis* Kunkel, 1910).

Ochlesidae Stebbing

Ochlesidae Stebbing, 1910:581.

Diagnosis.—Body compressed, at least pereonites 1–6 projecting dorsalwards as thin flat keel or formed in to flat plaques (*Meraldia*). Rostrum well developed. Antennae poorly developed, short, flagella with 4 or fewer articles; accessory flagellum absent. Mouthpart field conically developed. Epistome and labrum narrow, long, entire. Incisor of mandible ordinary, toothed, or needle-shaped or blunt or scarcely toothed; raker row absent; molar small and weakly triturative or reduced and simple; palp always present, 3-articulate, D–E setae reduced. Lower lip without inner lobes, outer lobes very thin, with inner notches only at apices. Inner plate of maxilla 1 minute, often medially setose, setae usually very small; outer plate coniform, spinal margin very oblique, spines few and mostly fused; palp tiny, 1-articulate. Inner plate of maxilla 2 with only terminal setae. Plates of maxilliped very thin, palp 0–2-articulate. Coxae 1–3 more or less acuminate, at least one coxa tapering, ventral margins not fitting normal ventral parabolic curve of anterior coxae; coxae 1 and 4 shortened, coxa 3 usually with posterodorsal buttress, coxa 4 with peculiar shape (see figures in Coleman and Barnard 1991a), with posteroventral lobe, coxa 5 about as long as 4. Gnathopods feeble and with elongate articles 5–6 (article 3 of gnathopod 1 mostly elongate, versus Odiidae), gnathopod 1 weakly flagellar, gnathopod 2 usually slightly broader and shorter than gnathopod 1; gnathopods 1–2 simple, merus and carpus of gnathopod 2 produced. Article 2 of pereopods 5–7 lacking posterior cusps or teeth. Epimeron 3 rarely with 2 large cusps. Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 subequal to or longer than peduncle, flattened, lanceolate, usually 1-articulate. Telson entire, generally not longer than peduncle of uropod 3.

Relationship.—Differing from the Epimeriidae in the thin dorsal keel or plaques on the pereon, short antennal flagella, short coxae 1 and 4, in the simple gnathopod 1 and produced merus and carpus of gnathopod 2, reduction of D–E setae on the mandibular palp, reduction of medial maxillary setae and loss of at least 2 articles on the maxillipedal palp. See Epimeriidae for mention of differences from families outside of the families included herein.

Differing from the Odiidae in the reduction of coxae 1 and 4, absence of rakers, in

the produced carpus of gnathopod 2 and the simple gnathopod 1.

Differing from the Acanthonotozomatidae in the presence of a molar, and from that family and Acanthonotozomellidae in the reduction of the maxillipedal palp, reduction of D–E setae on the mandibular palp, reduced coxae 1 and 4, and the produced carpus of gnathopod 2.

Differing from the Iphimediidae in the produced carpus of gnathopod 2, simple gnathopods 1–2, short coxae 1 and 4, keel-like dorsal margin of pereonites 5–6, and the presence of a mandibular molar.

Differing from the Dikwidae in the more or less well developed head, short coxa 4, simple gnathopod 1, produced carpus of gnathopod 2, conical outer plate of maxilla 1, reduced palp of maxilliped, and the reduced D–E setae of the mandibular palp.

Like the Ochlesidae, the Lafystiidae have a 2-articulate palp on the maxilliped; otherwise they differ from Ochlesidae in the long coxa 4, normal lower lip, broad, unkeeled body, parachelate gnathopod 2, lack of meral and carpal lobe on gnathopod 2 and well developed laciniae mobiles on both mandibles.

List of genera.—*Ochlesis* Stebbing, 1910 (=type genus); *Curidia* Thomas, 1983; *Meraldia* Barnard & Karaman, 1987; *Ochlesodius* Ledoyer, 1982.

Dikwidae, new family

Type genus.—*Dikwa* Griffiths, 1974:266.

Diagnosis.—Body compressed, with thin middorsal keel on pereonites 1–5, dorsal carina on pereonites 6–7 and pleonites 1–3 (based on new observation of material from South African Museum). Head poorly formed, rostrum absent (our interpretation despite Griffiths 1977). Antennae elongate, flagella with 5+ articles; accessory flagellum absent. Mouthpart part field ?quadrately developed (box-like). Epistome and labrum broad, short, incised. Incisor of mandible ordinary, toothed; raker row strong; molar large and triturative; palp 3-articulate (D–E setae well developed, versus Odiidae). Lower lip without inner lobes, without inner notches. Inner plate of maxilla 1 slender, only apically setose; outer plate truncate, with 13 spines; palp large, 2-articulate. Inner plate of maxilla 2 [unknown]. Palp of maxilliped 4-articulate, article 2 not produced medially. Coxae 3–4 more or less acuminate, coxa 2 shortened and blunt below, ventral margins not fitting normal ventral parabolic curve of anterior coxae; coxae 1 and 4 not shortened, coxa 1 truncate-concave below, with marginal points and anteroventral lobule, coxa 4 with small posteroventral lobe, coxa 5 shorter than posteroventral lobe of 4. Gnathopods feeble and with elongate articles 5–6 on gnathopod 2, and article 6 on gnathopod 1, gnathopod 2 flagellar and much longer than gnathopod 1; gnathopod 1 propodochelate, gnathopod 2 simple, merus and carpus not produced. Article 2 of pereopods 5–7 with posterior cusps or teeth. Epimeron 3 lacking 2 large cusps posteroventrally. Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 longer than peduncle, though peduncle elongate, flattened, lanceolate, 1-articulate. Telson weakly incised, not longer than peduncle of uropod 3.

Relationship.—Differing from Epimeriidae in the severely reduced head, chelate gnathopod 1, simple gnathopod 2, and elongate articles of the gnathopods.

Differing from Odiidae in the acuminate coxae 3–4, simple gnathopod 2, conical outer plate of maxilla 1, broad (ordinary) lower lip, and broad prebuccal parts.

Differing from Ochlesidae in the reduced head, chelate gnathopod 1, well developed and extraordinary maxilla 1, 4-articulate maxillipedal palp, well developed antennal flagella, and unshortened coxae 1 and 4.

Differing from the Acanthonotozomatidae and Acanthonotozomellidae in having a mandibular molar, chelate gnathopod 1, flagellar gnathopod 2 and reduced head.

Differing from Iphimediidae in the sim-

ple gnathopod 2, presence of mandibular rakers, triturative molar, normal lower lip, and severely reduced head.

See Epimeriidae for mention of differences from families outside of the families included herein.

List of genera.—*Dikwa* Griffiths, 1974.

Iphimediidae

Iphimedinae Boeck, 1871:178.

Diagnosis.—Body compressed, with dorsal teeth (except minutely in *Iphimedia gibba* and absent in *Pariphimedia normani*). Rostrum well developed. Antennae elongate, flagella with 5+ articles; accessory flagellum 0–1 articulate. Mouthpart part field conically developed. Epistome and labrum highly variable, broad or narrow, short or long, incised or entire. Incisor of mandible variable, broad and toothed in transition to needle shaped or blunt, untoothed, callused or hollowed out; raker row absent; molar absent or reduced (*Stegopanoploea* with conical molar); palp always present, 3-articulate. Lower lip without inner lobes, with or without distinct inner notches. Inner plate of maxilla 1 ordinary or minute, usually medially setose; outer plate oblique, normally spinose or reduced (*Nodotergum*); palp large or small, 1–2-articulate. Inner plate of maxilla 2 rarely with facial setae. Palp of maxilliped 3–4-articulate, article 2 produced medially in several genera. Coxae 2–4 more or less acuminate, ventral margins fitting normal ventral parabolic curve of anterior coxae; coxae 1 and 4 not shortened, coxa 1 variable, broad or narrow, acuminate or not, coxa 4 with large posteroventral lobe, coxa 5 shorter than 4. Gnathopods feeble and with elongate articles 5–6, gnathopod 1 often flagellar, gnathopod 2 usually slightly longer or stouter than gnathopod 1; gnathopods 1–2 propodochelate, or gnathopod 1 simple in *Nodotergum,* merus and carpus not produced. Article 2 of pereopods 5–7 often with posterior cusps or teeth. Epimeron 3 usually with 2 large cusps. Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 longer than peduncle, flattened, lanceolate, 1-articulate. Telson entire or weakly incised, generally not longer than peduncle of uropod 3.

Remarks.—Gnathopod 1 of *Nodotergum* is simple, and because rakers and notches on lower lip are absent, *Nodotergum* might be assigned to Acanthonotozomatidae, but the chelate gnathopod 2 and 3-articulate maxillipedal palp suggest closer affinities to Iphimediidae than to Acanthonotozomatidae. The outer plate of maxilla 1 in *Nodotergum* is reduced and poorly spinose. *Maxilliphimedia* and *Paranchiphimedia* differ from typical Iphimediidae in the untapered coxa 1 and broad, flattened mandible.

Relationship.—Differing from the Epimeriidae in the absence of raker spines and the presence of at least one pair of chelate gnathopods.

Differing from the Odiidae in the chelate gnathopod 2, reduction or absence of mandibular molar, and absence of rakers.

The maxillipedal palp of Ochlesidae is 0–2 articulate, the antennal flagella are reduced, coxae 1 and 4 are shortened, the propodi of the gnathopods are simple, and gnathopod 2 otherwise has lobate merus and carpus.

Differing from the Acanthonotozomatidae in the presence of at least one pair of chelate gnathopods.

Differing from the Acanthonotozomellidae in the presence of at least one pair of chelate gnathopods and the absence of rakers.

Differing from the Dikwidae in the chelate gnathopod 2, unreduced head and the reduced or absent mandibular molar and rakers.

Differing from Stilipedidae in the chelate gnathopod 2.

See Epimeriidae for mention of differences from families outside of the families included herein.

Removals.—*Bathypanoploea* and its synonyms are removed to the Stilipedidae.

List of genera.—*Iphimedia* Rathke, 1843 (type genus) =*Microcheles* Kroyer, 1846, =*Panoploea* Thomson, 1880, =*Iphimediopsis* Della Valle, 1893, =*Cypsiphimedia* K. H. Barnard, 1955; *Anchiphimedia* K. H. Barnard, 1930; *Anisoiphimedia* Karaman, 1980; *Coboldus* Krapp-Schickel, 1974; *Echiniphimedia* K. H. Barnard, 1930; *Gnathiphimedia* K. H. Barnard, 1930; *Iphimediella* Chevreux, 1911, 1912b; *Labriphimedia* K. H. Barnard, 1931, 1932 (=*Maoriphimedia* Hurley, 1954); *Maxilliphimedia* K. H. Barnard, 1930; *Nodotergum* Bellan-Santini, 1972; *Paranchiphimedia* Ruffo, 1949; *Parapanoploea* Nicholls, 1938; *Pariphimedia* Chevreux, 1906; *Pseudiphimediella* Schellenberg, 1931; *Stegopanoploea* Karaman, 1980.

Odiidae, new family

Type genus.—*Odius* Liljeborg, 1865:11.

Diagnosis.—Body compressed, all pereonites dorsally flush, in most species projecting dorsalwards as thin flat keel (see "Remarks" below), teeth present only on pleon. Rostrum well developed. Antennae poorly developed, short, flagella with 6–8 short articles; accessory flagellum absent. Mouthpart part field conically developed. Epistome and labrum narrow, elongate, minutely incised. Incisor of mandible narrow, scarcely toothed; raker row strong; molar small and triturative; palp present, 3-articulate (D–E setae reduced, versus Dikwidae). Lower lip without inner lobes, outer lobes thin, with inner notches or excavations. Inner plate of maxilla 1 small, apically with 1–3 setules; outer plate oblique ("conical"), normally spinose; palp 1-articulate. Inner plate of maxilla 2 without facial or medial setae. Palp of maxilliped 4-articulate, article 2 not produced medially. Coxae 1–3 weakly tapering but coxae 2–4 remaining quadrate below, ventral margins fitting normal ventral parabolic curve of anterior coxae; coxae 1 and 4 not shortened, coxa 3 lacking posterodorsal buttress, coxa 4 with large posteroventral lobe, coxa 5 shorter than 4. Gnathopod 1 feeble and with elongate articles 5–6, weakly flagellar, gnathopod 2 much larger and broader than gnathopod 1; gnathopod 1 propodochelate or with spine forming chela; 2 propodosubchelate, merus and carpus produced. Article 2 of pereopods 5–7 with or without posterior cusps or teeth. Epimeron 3 with 2 large cusps posteroventrally. Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 longer than peduncle, flattened, lanceolate, usually 1-articulate. Telson weakly incised, not longer than peduncle of uropod 3.

Remarks.—We have examined the types of *O. antarcticus* which have a thin but weak dorsal keel from pereonite 5 to pleonite 2.

Relationship.—Differing from Epimeriidae in the diverse gnathopods, with chelate gnathopod 1 and produced merus and carpus on gnathopod 2, conically arranged mouthparts and generally reduced subsidiary features on mouthparts, the presence of distinct notches or medial excavations on the lobes of the lower lip, and a flush dorsal keel on the pereon.

Odius has many of the same body formations as found in Ochlesidae. For example, its basic members, albeit weakly in *O. antarcticus,* have the compressed body formed into a dorsal keel and have a dorsal tooth on pleonite 3 characteristic of primitive ochlesids (compare *O. carinatus* and *O. eridunda*). The head is tall dorsoventrally and short anteroposteriorly and incipiently appears to be telescoped into pereonite 1. The antennae are short and the flagella poorly articulate. The labrum is slender, elongate and triangular. The mandibular molar is strongly processed, and the number of D and E setae on the third palp article is reduced (a character not otherwise used in diagnoses except for Odiidae and Ochlesidae). *Odius,* is, however, not an ochlesid because articles 4–6 of gnathopod 2 are short and broad, and the propodus is broadly subchelate; article 3 of gnathopod 1 is not elongate and the propodus is cheliform; coxa 4

is fully developed and lobate as in Iphimediidae; the maxillipedal palp has more than 2 articles; coxa 1 is not significantly reduced in size. Differing from the Ochlesidae also in the truncate coxae 2–3 and presence of cusps on article 2 of pereopods 5–7.

Differing from the Acanthonotozomatidae, Acanthonotozomellidae, and Iphimediidae (except *Stegopanoploea*) in the presence of a molar, the produced merus and carpus of gnathopod 2, and the absence of dorsal teeth on the pereon; instead, the pereon has a flush dorsal keel or margin.

The Dikwidae are characterized by reduced head, well developed D–E setae on the mandibular palp, and flagellar gnathopod 2.

See Epimeriidae for mention of differences from families outside of the families included herein.

List of genera.—*Odius* Liljeborg, 1865 (=*Otus* Bate, 1862, homonym, Lepidoptera) (=type genus); *Postodius* Hirayama, 1983.

Astryidae

Astryidae Pirlot, 1934:175.

Diagnosis.—Body compressed, with or without dorsal teeth (sometimes confined to metasome). Rostrum of medium size or very small. Antennae weakly elongate, flagella with 5+ articles; accessory flagellum absent. Mouthpart part field quadrately developed (box-like). Epistome and labrum broad, short, weakly incised. Incisor of mandible ordinary, toothed; raker row strong; molar reduced, conical and pubescent; palp always present, 3-articulate. Lower lip without inner lobes (except tiny inner basal lobes), outer lobes widely spaced, without distinct inner notches. Inner plate of maxilla 1 ordinary, somewhat medially setose; outer plate oblique, spines reduced to 7 (? or 8) in *Eclysis*; palp large, 2-articulate. Inner plate of maxilla 2 without facial setae. Palp of maxilliped 4-articulate, article 2 not produced medially. Coxae 2–4 scarcely acuminate, ventral margins fitting normal ventral parabolic curve of anterior coxae; coxae 1 and 4 not shortened, coxa 1 expanded, wider than coxa 2, truncate or rounded below, coxa 4 with posteroventral lobe, coxa 5 shorter than 4. Gnathopods feeble, simple, merus not lobate, with slightly elongate, weakly lobate or non-lobate carpus, propodus shorter and narrower than carpus, nipple-like, gnathopod 2 usually slightly longer than gnathopod 1. Article 2 of pereopods 5–7 lacking posterior cusps or teeth. Epimeron 3 lacking 2 large cusps. Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 longer than peduncle, flattened, lanceolate, usually 1-articulate. Telson cleft.

Relationship.—Differing from Stilipedidae in the narrowness of the incisors, the presence of a setose molar and the reduction of spines on the outer plate of maxilla 1.

Remarks.—We keep *Eclysis* distinct from *Astrya* based on the expanded palp of maxilla 1 and the need to describe many unknown characters. *Epimeriella* is transferred to Epimeriidae because of the ordinary outer plate of maxilla 1 and poorly dominant carpus of the gnathopods. *Epimeriella victoria* Hurley (1957) is transferred to *Epimeria* because of tapering coxa 1.

List of genera.—*Astyra* Boeck, 1871 (=*Chagosia* Walker, 1909, =*Parastyra* Pirlot, 1934); *Eclysis* K. H. Barnard, 1932.

Stilipedidae

Stilipedidae Holmes, 1908:535.

Diagnosis.—Body compressed, dorsal teeth present or confined to urosome. Rostrum very small. Antennae moderately elongate, flagella with 5+ articles; accessory flagellum 0–1 articulate. Mouthpart part field quadrately developed (box-like). Epistome and labrum broad, short, incised or lobate. Incisor of mandible extremely wide, smooth or toothed; raker row present or

absent; molar absent; palp always present, 3-articulate. Lower lip with or without weak inner lobes, outer lobes widely separated, without distinct inner notches. Inner plate of maxilla 1 ordinary, apically and somewhat medially setose; outer plate oblique, normally spinose in 2 genera, very wide and superspinose in many species; palp large, 2-articulate, greatly widened apically. Inner plate of maxilla 2 without facial setae. Palp of maxilliped 4-articulate, article 2 not produced medially. Coxae 2–4 more or less acuminate, ventral margins flush; coxae 1 and 4 not shortened, coxa 1 widely expanded, wider than narrowed coxa 2, ventral margin rounded or quadrate, coxa 4 weakly acuminate, with posteroventral lobe, coxa 5 shorter than 4. Gnathopods feeble, simple or very poorly subchelate, merus not lobate, with slightly elongate, weakly lobate carpus, propodus irregularly ovate, shorter and narrower than dominant carpus, gnathopod 2 usually slightly longer than gnathopod 1. Article 2 of pereopods 5–7 without posterior cusps or teeth. Epimeron 3 lacking 2 large cusps. Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 longer than peduncle, flattened, lanceolate, 1-articulate. Telson weakly incised.

Remarks.—*Astryoides* and *Bathypanoploea* retain the plesiomorphic characters of rakers and normal outer plate of maxilla 1.

Relationship.—See Astryidae and Acanthonotozomellidae Relationships. Differing from the Iphimediidae and Acanthonotozomatidae in the broadened and non-acuminate coxa 1. Differing from Epimeriidae in the lack of molar, broad, flat mandible, and dominant carpus of the gnathopods.

List of genera.—*Stilipes* Holmes, 1908 (type genus); *Bathypanoploea* Schellenberg, 1939 (=*Iphimediopsis* Schellenberg, 1931, homonym, =*Epimeriopsis* K. H. Barnard, 1931, void ab initio, misidentified type species, =*Pseudiphimediopsis* Ruffo, 1949); *Alexandrella* Chevreux, 1911, 1912b (=*Parandaniexis* Nicholls, 1938, =homonym, =*Pseudandaniexis* Nicholls, 1938); *Astyroides* Birstein & Vinogradova, 1960.

Lafystiidae

Lafystiidae Sars, 1895:382.

Diagnosis.—Body broadened, without dorsal teeth. Rostrum large, flattened. Antennae scarcely elongate, flagella with 5+ articles; accessory flagellum absent. Mouthpart part field conically developed (box-like). Epistome and labrum of ordinary width and length, entire. Incisor of mandible ordinary, toothed; raker row absent; molar absent; palp present, 3-articulate. Lower lip without inner lobes, without distinct inner notches. Inner plate of maxilla 1 small, apically setose; outer plate oblique, normally spinose; palp tiny, 1-articulate. Inner plate of maxilla 2 without facial setae. Palp of maxilliped reduced to 2 articles. Only coxae 4–6 acuminate, coxa 4 longer than coxae 1–3, latter ordinary and quadrate, their ventral margins flush; coxa 4 with weak posteroventral lobe, with strong anteroventral lobe, coxae 5–6 with strong, sharp posteroventral lobe, scarcely shorter than or subequal to 4. Gnathopod 1 feeble and with scarcely elongate articles 5–6, gnathopod 2 slightly larger than gnathopod 1; gnathopod 1 simple, gnathopod 2 weakly propodochelate, merus and carpus not produced. Article 2 of pereopods 5–7 without posterior cusps or teeth. Epimeron 3 lacking 2 large cusps. Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 elongate but peduncle also slightly elongate, rami flattened, lanceolate, 1-articulate. Telson entire, not longer than peduncle of uropod 3.

Relationship.—Differing from the Laphystiopsidae in the normal outer plate of maxilla 1, the reduction of the maxillipedal palp, the sub(para)chelate gnathopod 2, and the lack of molar.

List of genera.—*Lafystius* Kroyer, 1842 (type genus) (=*Darwinia* Bate, 1857, =*Der-*

mophilus Beneden & Bessels, 1870, =*Ichthymozocus* Hesse, 1873).

Laphystiopsidae

Laphystiopsidae Stebbing, 1899:211.

Diagnosis based only on *Laphystiopsis*; see Remarks for *Prolaphystius*.

Diagnosis.—Body slightly broadened, with weak or strong dorsal teeth on few pleonites. Rostrum large and flat or absent. Antennae elongate, first longer than second, flagella with 5+ articles; accessory flagellum absent. Mouthpart part field quadrately developed (box-like). Epistome and labrum broad, short, minutely incised. Incisor of mandible ordinary, toothed; rakers absent; molar present, well developed but smooth or triturative (*Prolaphystius*); palp present, 3-articulate. Lower lip with or without small fleshy inner lobes, without distinct inner notches. Inner plate of maxilla 1 small, with one apical seta; outer plate oblique, spines reduced to 5; palp large, 1–2-articulate. Inner plate of maxilla 2 without facial setae. Palp of maxilliped 4-articulate, article 2 not produced medially. No member of coxae 1–4 acuminate downward, all short, broader than long, ventral margins of coxae 1–4 flush; coxa 4 without posteroventral lobe; coxa 5 longer or shorter than 4. Gnathopods 1–2 feeble, simple, carpi not lobate, propodi narrow and rectangular. Article 2 of pereopods 5–7 lacking posterior cusps or teeth. Epimeron 3 lacking 2 large cusps. Urosomites free. Uropods 1–3 biramous. Rami of uropod 3 elongate, peduncle ordinary, rami flattened, lanceolate, 1-articulate. Telson entire, not longer or greatly longer than peduncle of uropod 3.

Remarks.—*Prolaphystius* combines characters of Lafystiidae and Laphystiopsidae. Its lafystiid characters are larger coxae with some degree of acumination, a posterior lobe on coxa 4, and shortened coxa 5; its laphystiopsid characters are presence of (triturative) molar, simple feeble gnathopod 2, and reduction of spines on outer plate of maxilla 1; its unique apomorphic characters are elongate telson, and loss of rostrum. K. H. Barnard (1930:342) thought that Lafystiidae and Laphystiopsidae should be synonymized. We believe *Prolafystius* should be reevaluated and place it here only provisionally.

Relationship.—Differing from Lafystiidae in the presence of a molar, reduction of spines on outer plate of maxilla 1, simple gnathopod 2, and 4-articulate palp of the maxillipeds.

List of genera.—*Laphystiopsis* Sars, 1895 (type genus); ?*Prolaphystius* K. H. Barnard, 1930; *Prolaphystiopsis* Schellenberg, 1931. (Note: We have determined that Sars (1895) overlooked the biarticulate condition of the palp on maxilla 1 in *Laphystiopsis*; this negates the only published distinction of *Prolaphystiopsis* Schellenberg; specimens of the latter will be examined to seek any other possible generic difference).

Acknowledgments

The authors are grateful to Dr. Les Watling and five referees for valuable improvements.

Literature Cited

Andres, H. G. 1985. Die Gammaridea (Crustacea: Amphipoda) der deutschen Antarktis-Expeditionen 1975/1976 und 1977/1978. 4. Acanthonotozomatidae, Paramphithoidae und Stegocephalidae.—Mitteilungen aus den Hamburgischen Zoologischen Museum und Zoologisches Institut 82:119–153.

Barnard, J. L. 1969. The families and genera of marine gammaridean Amphipoda.—United States National Museum, Bulletin 271:1–535.

———, & G. S. Karaman. 1987. Revisions in classification of gammaridean Amphipoda (Crustacea) Part 3.—Proceedings of the Biological Society of Washington 100:856–875.

Barnard, K. H. 1930. Amphipoda.—British Antarctic ("Terra Nova") Expedition, 1910. Natural History Reports, Zoology 8:307–454.

———. 1931. Diagnosis of new genera and species of amphipod Crustacea collected during the

'Discovery' investigations, 1925–1927.—Annals and Magazine of Natural History (10)7:425–430.

———. 1932. Amphipoda.—Discovery Reports 5:1–326.

———. 1955. Additions to the fauna-list of South African Curstacea and Pycnogonida.—Annals of the South African Museum 43:1–107.

Bate, C. S. 1862. Catalogue of the specimens of amphipodous crustacea in the collection of the British Museum. British Museum (Natural History), London, iv + 399 pp., pls. 1, 1a, 2–58.

Bellan-Santini, D. 1972. Invertebres marine des XIIeme et XVeme Expeditions antarctiques francaises en Terre Adelie 10. Amphipodes Gammariens.—Tethys Supplement 4:57–238.

Beneden, E. van, & E. Bessels. 1870. Memoire sur la formation du blastoderme chez les amphipodes, les lerneens et les copepodes.—Memoires Savants Etrangers, Academie Royal Science Lettres Beaux-arts Belgique 34(4):1–59. [See footnote in this paper.]

Birstein, J. A., & N. G. Vinogradova. 1960. Donnye ultraabissal'nye gammaridy severo-zapadnoi chasti Tixogo Okeana. I. Semeistva Liljeborgiidae, Astryidae, Lepechinellidae, Gammaridae.—Akademiia Nauk SSSR, Instituta Okeanologii, Trudy 34:147–164.

Boeck, A. 1871. Crustacea Amphipoda Borealia et Arctica.—Forhandslinger i Videnskabs-Selskabet i Christiania 1870:3–280.

———. 1876. De Skandinaviske og Artiske Amphipoder. A. W. Brogger, Christiania, iv + 712 pp., 32 pls.

Bruzelius, R. M. 1859. Bidrag till kannedomen om skandinaviens Amphipoda Gammaridea.—Kongliga Svenska Vetenskaps-Akademiens Handlingar, new series 3:1–104.

Chevreux, E. 1906. Crustaces amphipodes.—Expedition Antarctique Francaise (1903–1905) commandee par le Dr. Jean Charcot. Sciences Naturelles, Documents Scientifiques 1–100, 56 figs.

———. 1911. Sur les amphipodes des Expeditions Antarctiques Francaises.—Academie des Sciences, Paris, Comptes Rendus 153:1166–1168.

———. 1912a. Diagnoses d'amphipodes nouveaux. Deuxieme Expedition dans l'Antarctique, dirigee par le Dr. Charcot, 1908–1910.—Bulletin du Museum d'Histoire Naturelle, Paris 18:208–218.

———. 1912b. Amphipodes.—Deuxieme Expedition Antarctique Francaise (1908–1910) commandee par le Dr. Jean Characot, Sciences Naturelles, Documents Scientifiques 79:186, 62 figs.

Coleman, C. O., & J. L. Barnard. 1991a. *Curidia magellanica,* new species, from Magellan Strait (Crustacea: Amphipoda: Ochlesidae).—Proceedings of the Biological Society of Washington 104:269–278.

———. 1991b. *Amatiguakius forsberghi,* a new genus and species from Alaska (marine Amphipoda: Epimeriidae).—Proceedings of the Biological Society of Washington 104:279–287.

Costa, A. 1851. Pp. 44–47, fig. 2 *in* Gugl. Hope's Catalogo dei Crostacei Italiani e di Molti Altri del Mediterraneo. Azzolino, Napoli.

———. 1851–1853. Fauna del Regno di Napoli [and] Catalogo de' Crostacei del Regno di Napoli. [Miscellaneous pages of incomplete editions seen; see Stebbing 1888:247–250.]

Della-Valle, A. 1893. Gammarini del Golfo di Napoli.—Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte, Monographie 20:xi + 948 pp., atlas (Atlante) of 61 pls.

Griffiths, C. L. 1974. The Amphipoda of southern Africa part 4. The Gammaridea and Caprellidea of the Cape Province east of Cape Agulhas.—Annals of the South African Museum 65:251–336.

———. 1977. The South African Museum's Meiring Naude Cruises Part 6 Amphipoda.—Annals of the South African Museum 74:105–123.

Gurjanova, E. 1955. Novye vidy bokoplavov (Amphipoda, Gammaridea) iz severnoi chasti Tixogo Okeana.—Zoologicheskogo Instituta Akademii Nauk SSSR, Trudy 18:166–218.

Heller, C. 1875. Die Crustaceen, Pycnogoniden und Tunicaten der K. K. Osterr.-Ungar. Nordpol-Expedition [sic].—Denkschriften der Kaiserliche Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Classe 25:25–46, 5 pls.

Hesse, M. 1873. Memoire sur des crustaces rares ou nouveaux des cotes de France.—Annales des Sciences Naturelles, 5 serie, Zoologie et Paleontologie 17(7):1–16.

Hirayama, A. 1983. Taxonomic studies on the shallow water gammaridean Amphipoda of west Kyushu, Japan. I. Acanthonotozomatidae, Ampeliscidae, Ampithoidae, Amphilochidae, Anamixidae, Argissidae, Atylidae and Colomastigidae.—Publications on the Seto Marine Biological Laboratory 28:75–150.

Holmes, S. J. 1908. The Amphipoda collected by the United States Bureau of Fisheries Steamer, "Albatross", off the west coast of North America, in 1903 and 1904, with descriptions of a new family and several new genera and species.—Proceedings of the United States National Museum 35:489–543.

Hurley, D. E. 1954. Studies on the New Zealand amphipodan fauna no. 9. The families Acanthonotozomatidae, Pardaliscidae and Liljebor-

giidae.—Transactions of the Royal Society of New Zealand 82:763–802.

———. 1957 Some Amphipoda, Isopoda and Tanaidacea from Cook Strait.—Zoology Publications Victoria University Collections 21:1–20.

Karaman, G. S. 1980. Revision of the genus *Iphimedia* Rathke 1843 with description of two new genera, *Anisoiphimedia* and *Stegopanoploea,* n. gen. (Fam. Acanthonotozomatidae).—Poljoprivreda I Sumarstvo, Titograd 26:47–72.

Krapp-Schickel, G. 1974. Camill Hellers Sammlung adriatischer Amphipoden—1866 und Heute.—Annalen der Naturhistorisches Museum, Wien 78:319–379.

Kroyer, H. 1842. Une nordiske Slaegter og Arter af Amfipodernes Orden, henhorende til Familien *Gammarina.* (Forelobigt Uddrag af et storre Arbejde).—Naturhistorisk Tidsskrift 4:141–166.

———. 1846. Karcinologiske Bidrag (Fortsaettelse).—Naturhistorisk Tidsskrift 2:1–211, pls. 1–2, 1–88, 115–123 [for amphipods only].

Kunkel, B. W. 1910. The Amphipoda of Bermuda.—Transactions of the Connecticut Academy of Arts and Sciences 16:1–116.

Ledoyer, M. 1982. Crustaces amphipodes gammariens familles des Acanthonotozomatidae a Gammaridae.—Faune de Madagascar 59(1):1–598.

Liljeborg, W. 1865. Bidrag till kannedomen om underfamiljen *Lysianassina* inom underordningen *Amphipoda* bland kraftdjuren.—["Nova Acta Regiae Societatis Scientiarum Upsaliensis III Serie"] [journal title from Stebbing 1888, only an unattributed reprint seen].

Moore, H. B. 1985. A new deep water species of Amphipoda (Crustacea) discovered off Otago, New Zealand and a note on another little known species.—Zoological Journal of the Linnean Society 83:229–240.

Nicholls, G. E. 1938. Amphipoda Gammaridea.—Australasian Antarctic Expedition 1911–14, Scientific Reports, C.-Zoology and Botany 2(4): 1–145.

Pirlot, J. M. 1934. Les amphipodes de l'expedition du Siboga. Deuxieme partie. . . . II. -Les amphipodes de la mer profonde. 2. Hyperiopsidae . . . Jassidae.—Siboga-Expeditie 33d:167–235.

Rathke, H. 1843. Beitrage zur Fauna Norwegens.—Verhandlungen Kaiserlichen Leopoldinisch-Carolinischen Akademie Naturforscher, Breslau 20(1):1–264, 264b, 264c, 12 pls. [Amphipoda:63–98, pls. 3, 4.]

Ross, J. C. 1835. Zoology. Pp. vii–c, pls. A–C, Appendix to the narrative of a second voyage in search of a north west passage, and of a residence in the Arctic regions during the years 1829, 1830, 1831, 1832, 1833. By Sir John Ross, C.B., K.S.A., K.C.S., &c.&c. Captain in the Royal Navy. Including the reports of Commander, now Captain, James Clark Ross, R.N., F.R.S., F.L.S., &c. and the discovery of the northern magnetic pole. A. W. Webster, London.

Ruffo, S. 1949. Amphipodes (II).—Resultats du voyage de la Belgica en 1897–99. . . . Rapports Scientifiques, Zoologie: 1–58, 18 figs.

Sars, G. O. 1895. Amphipoda. An account of the Crustacea of Norway with short descriptions and figures of all the species 1:viii and 711 pp., 240 pls., 8 suppl. pls. Alb. Cammermeyers, Christiania, Norway.

Schellenberg, A. 1926. Die Gammariden der deutschen Sudpolar-Expedition 1901–1903.—Deutsche Sudpolar-Expedition 18:235–414.

———. 1931. Gammariden und Caprelliden des Magellangebietes, Sudgeorgiens und der Westantarktis.—Further Zoological Results of the Swedish Antarctic Expedition 1901–1903 2(6):1–290.

———. 1939. Amphipoden des Kongo-Mundungsgebietes.—Revue de Zoologie et de Botanique Africaines 32:122–138.

Stebbing, T. R. R. 1888. Report on the Amphipoda collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–1876, Zoology 2:xxiv + 1737 pp., Eyre and Spottiswoodie, London.

———. 1899. Revision of Amphipoda (continued).—Annals and Magazine of Natural History (7)4:205–211.

———. 1906. Amphipoda I. Gammaridea.—Das Tierreich 21:1–806.

———. 1910. Crustacea. Part V. Amphipoda. Scientific Results Trawling Expedition H.M.C.S. "Thetis".—Australian Museum, Memoir 4 2: 565–658, pls. 47*–60*. [Asterisks denote special plates.]

Stock, J. H. 1974. The systematics of certain Ponto-Caspian Gammaridae (Crustacea, Amphipoda).—Mitteilungen Hamburg Zoologisches Museum Institut 70:75–95.

Thomas, J. D. 1983. *Curidia debrogania,* a new genus and species of amphipod (Crustacea: Ochlesidae) from the barrier reefs of Belize, Central America.—Proceedings of the Biological Society of Washington 96:127–133.

Thomson, G. M. 1880. A new species of Crustacea from New Zealand.—Annals and Magazine of Natural History (5)6:1–6.

Walker, A. O. 1906. Preliminary descriptions of new species of Amphipoda from the 'Discovery' Antarctic Expedition, 1902–1904.—Annals and Magazine of Natural History (7) 18:13–18.

———. 1907. Crustacea. III. Amphipoda.—National

Antarctic Expedition, British Museum (Natural History) 3:1–39.

———. 1909. Amphipoda Gammaridea from the Indian Ocean, British East Africa, and the Red Sea.—Transactions of the Linnean Society of London (2) Zoology 12:323–344.

Watling, L., & H. Holman. 1980. New Amphipoda from the Southern Ocean, with partial revisions of the Acanthonotozomatidae and Parampithoidae.—Proceedings of the Biological Society of Washington 93:609–654.

———, & M. H. Thurston. 1989. Antarctica as an evolutionary incubator: evidence from the cladistic biogeography of the amphipod family Iphimediidae. *In* J. A. Crane, ed., Origins and evolution of the antarctic biota.—Geological Society of America Special Publication 47:297–313.

(COC) Fachbereich 7, Zoomorphologie, Universitat Oldenburg, Postfach 2503, D-2900, Oldenburg, F.R.G.; (JLB) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 269–278

CURIDIA MAGELLANICA, NEW SPECIES, FROM MAGELLAN STRAIT (CRUSTACEA: AMPHIPODA: OCHLESIDAE)

C. O. Coleman and J. L. Barnard

Abstract.—The new species, *Curidia magellanica,* differs from similar species, *Curidia debrogania* and *Ochlesodius spinicornis,* in the strong development of the pointed projections on peduncular articles 1 and 2 of antenna 1 and the fourth article of antenna 2. The coxal plates of pereopods 2 and 3 of *Ochlesodius spinicornis* are apically truncate, in *Curidia magellanica,* rounded and subacute, respectively. The maxillipedal palp is much longer in the new species compared to *Curidia debrogania* and there are remnants of an articular suture, which might indicate relationships to the genus *Ochlesodius.* The classic genus *Odius* is an analogous morph in the Iphimediidae with many characters that might be considered plesiomorphic to the Ochlesidae; it has been relegated to a new family Odiidae by Coleman & Barnard (1991).

The genera and species of the family Ochlesidae are reviewed for the first time since its description by Stebbing (1910). A new diagnosis of the family is presented by Coleman & Barnard (1991), who also discuss its relationship to many similar families; here, a complete description of the family is presented. New keys for identification and lists of species are provided herein. The lists of species present each species with its describer and date followed in parentheses by one or more modern references, followed by geographical codes for distribution set in brackets; a list of these codes is found in Barnard & Barnard (1983:181–203).

Ochlesidae

Ochlesidae Stebbing, 1910:581.—Coleman & Barnard, 1991:259.

Description.—Body massive, compressed, one or more segments usually with large dorsal tooth. Head short from front to rear, but tall, partially enveloped by pereon. Rostrum large. Antennae short but thick, not longer than 5 pereonites, flagella sparsely articulate, accessory flagellum absent. Eyes ordinary. Lateral cephalic lobes well developed.

Mouthparts grouped conically. Labrum elongate. Mandibular incisors moderately broad, smooth or weakly crenulate in middle, each end (side) bounded by small tooth; left mandible with spiniform lacinia mobilis, right absent or represented by small conical spine; palp 3-articulate, article 1 elongate or not; rakers absent; molar very small, poorly triturative or simple. Mandibular lobes of labium acuminate, inner lobes weak or absent. Inner plate of maxilla 1 small or indiscernible, outer plate subconical, spines mostly fused to base, palp vestigial though often armed with long seta. Lobes of maxilla 2 elongate, inner shortened. Inner plate of maxilliped acuminate, outer operculiform; palp small, 0–2 articulate.

Anterior coxae acuminate or oddly shaped: coxae 1 and 4 shortened relative to long and thin coxae 2 and 3, coxa 3 with posterodorsal buttress forming attachment to pereon; coxa 5 shorter than 4. Gnathopods feeble, gnathopod 1 simple or minutely parachelate, gnathopod 2 simple or subchelate, otherwise gnathopod 2 with

produced carpus and/or merus; articles 3–6 of gnathopod 1 slender, elongate, apical setae usually strap-shaped or grossly feathered. Article 2 of pereopods 5–7 well expanded, with posteroventral lobe. Gills on coxae 2–7, narrow, or apically geniculate; oostegites narrow and broad together in same species, thus narrow on coxae 2 and 5 but broad on coxae 3–4 or also broad on coxa 2 in another species. Pleopods ordinary. Epimera toothed or not.

Urosomites separate. Uropods 1–3 biramous but outer rami of uropods 2–3 shorter than inner; peduncle of uropod 3 elongate, thus longer than urosomites 2–3 together, inner rami of uropod 3 as long as or slightly shorter than peduncle, flattened, lanceolate, outer ramus 1-articulate. Telson entire or weakly incised, variable in size and shape.

Variables.—Body narrowing dorsally to thin continuous keel or segments forming flattened dorsal pedestals. Antennae cuspidate or not. Epistome and labrum highly variable, broad or narrow, long or short, incised or entire. Coxae variable. Dactyls of pereopods 3–7 elongate (*Ochlesis innocens*), or short (*Ochlesis lenticulosus*). Telson short or elongate, leaf-shaped or long and truncate.

Relationship.—Ochlesidae differ from Iphimediidae in (1) the produced merus and carpus of gnathopod 2; (2) the reduction of the maxillipedal palp to fewer than 3 articles; (3) the reduced antennal flagella; (4) the slender keel-like narrowing of the dorsal margin of pereonites 1–6, which also lack teeth; and (5) the peculiar though internally diverse forms of the anterior coxae, in which coxa 4 is strongly shortened, coxa 1 is disparately shortened, and coxa 4 occurs in grotesque shapes. The shortened condition of coxa 1 is of incremental degree, in that the shortened coxa 1 of Iphimediidae remains within the smooth parabola formed by the lower edges of coxae 4, 3, 2, and 1, whereas in Ochlesidae, coxae 2 and 3 are of equal length; no parabolic curve with coxa 4 is possible because it is shortened in such fashion that the anterior coxae have a jagged appearance. The dorsal keel of the six anterior thoracic segments also is found in several members of Acanthonotozomatidae and in the genus *Dikwa* (Dikwidae), but in all of those, one or more of pereonites 1–6 has a dorsal tooth.

See Coleman & Barnard (1991) for additional comments on more remote taxa.

Key to the Genera of Ochlesidae

1. Palp of maxilliped 2-articulate ... . *Ochlesodius*
– Palp of maxilliped 0–1 articulate .. 2
2. Body keel dorsally flattened, with plaques, pereonites with lateral plaques, telson linguiform, lateral margins curled upward ..... *Meraldia*
– Body keel dorsally knife-like, pereonites smooth laterally, telson flat .. 3
3. Palp of maxilliped absent .... *Ochlesis*
– Palp of maxilliped 1-articulate ... . *Curidia*

Key to the Species of Ochlesidae

1. Body keel dorsally flattened, with plaques, pereonites with lateral plaques, telson linguiform, lateral margins curled upward .... *Meraldia meraldi*
– Body keel dorsally knife-like, pereonites smooth laterally, telson flat 2
2. Coxae 1–3 not tapering, blunt or truncate apically, palp of maxilliped with 2 articles . *Ochlesodius spinicornis*
– Coxae 1–3 tapering, rounded or attenuate apically, palp of maxilliped with 0–1 article 3
3. Coxa 4 not excavate posteriorly, body with at least one large dorsal tooth 4
– Coxa 4 excavate posteriorly, body lacking large dorsal teeth 7
4. Epimeron 3 with tooth 5
– Epimeron 3 lacking tooth 6

5. Pleonites 2–3 only with dorsal rugae ..... *Ochlesis innocens*
– Pleonites 2–3 with strong dorsal tooth ..... *Ochlesis lenticulosa*
6. Pereonite 7 and pleonites 1–2 with strong dorsal tooth, teeth present on antennae 1–2 ..... *Ochlesis carinata*
– Only pleonite 3 with strong dorsal tooth, teeth absent on antennae 1–2 ..... *Ochlesis eridunda*
7. Antennae and epimeron 3 lacking significant teeth .... *Ochlesis levetzowi*
– Antennae and epimeron 3 with significant teeth 8
8. Teeth of antennae small, palp of maxilliped absent ..... *Ochlesis alii*
– Teeth of antennae medium to large, palp of maxilliped 1-articulate 9
9. Palp of maxilliped shorter than basolateral margin of outer plate, flagellum of antenna 1 as long as articles 1–2 of peduncle, coxa 3 expanded distally from coxa 4, anterodorsal hump of coxae 3–4 small, pereonite 7 longer than pereonites 4–6 together, teeth of antennae of medium length ... *Curidia debrogania*
– Palp of maxilliped longer than basolateral margin of outer plate, flagellum of antenna 1 as long as article 1 of peduncle, coxa 3 not expanded distally from coxa 4, anterodorsal hump of coxae 3–4 large, pereonite 7 not longer than pereonites 5–6 together, teeth of antenna long ..... *Curidia magellanica*

Curidia Thomas

Curidia Thomas, 1983:127 (*Curidia debrogania* Thomas, 1983, original designation).

Diagnosis.—Like *Ochlesis* but maxilliped with 1-articulate palp.

Species.—*C. debrogania* Thomas, 1983, western Caribbean [471]; *C. magellanica* Coleman & Barnard, herein, Magellan region [864].

Marine, Caribbean Sea, Belize, 6 m, and Magellan region, 92–101 m, 2 species.

Meraldia Barnard & Karaman

Meraldia Barnard & Karaman, 1987:857 (*Ochlesis meraldi* J. L. Barnard, 1972, original designation).

Diagnosis.—As in key.

Species.—*Meraldia meraldi* (J. L. Barnard, 1972) southern Australia [785].

Marine, Pearson Islands, South Australia, 35 m, 1 species.

Ochlesis Stebbing

Ochlesis Stebbing, 1910:581 (*Ochlesis innocens* Stebbing, 1910, monotypy).

Diagnosis.—As in key.

Removal.—*Ochlesis meraldi* J. L. Barnard, 1972, to *Meraldia*.

Species.—*Ochlesis alii* J. L. Barnard, 1970 (?*O. innocens* ID of Pirlot, 1936 and ?Schellenberg, 1938), Hawaii and Indonesia [381 + ?640]; *O. carinatus* Ledoyer, 1986, Walters Bank, bathyal [725wB]; *O. eridunda* J. L. Barnard, 1972, southern Australia [785]; *O. innocens* Stebbing, 1910, southeast Australia [781]; *O. lenticulosus* K. H. Barnard, 1940 (Griffiths 1974b, 1974c, 1975), southern Africa [743]; *O. levetzowi* Schellenberg, 1953 (Griffiths 1974a, 1974c), southern Africa [743].

Marine, Indo-Pacific from Hawaii to southern Australia and southern Africa, 0–200 m, 6 species.

Ochlesodius Ledoyer

Ochlesodius Ledoyer, 1982:48 (*Ochlesodius spinicornis* Ledoyer, 1982, original designation).

Diagnosis.—As in key.

Species.—*Ochlesis spinicornis* Ledoyer, 1982, Madagascar [698].

Marine, Glorieuses, 26 m, 1 species.

Curidia magellanica, new species
Figs. 1–4

Material.—Holotype, USNM 253546, female 2.4 mm, with setose oostegites; USNM 253547, 34 paratypes.

Type locality.—*Eltanin* St. 958 (52°56′S 75°00′W), Magellan region of south Chile; 5 Feb 1964; depth range 92–101 m; gear: 5′ Blake trawl.

Etymology.—The species name refers to the type locality.

Description.—Body strongly compressed laterally, sharply ridged dorsally as shown in Fig. 1a; pereonite 1 forming a rostrum-like anterior process; pereonite 2 shortest; pereonite 7 longest, posterodorsal margin forming a tooth; pleonites 1 and 2 posterolateral margin roundly produced, posteroventral angle of epimera produced, posterodorsal margin slightly produced; pleonite 3 with dorsal hump, posteroventral margin of epimeron 3 with pointed tooth, urosomite 1 longest; urosomite 2 shortest. Head partially hidden by pereonite 1, eyes with 17 to 22 ommatidia, lateral cephalic lobe pointed anteriorly; rounded epistomal process between antennae 2.

Antenna 1 (Fig. 1b): article 1 broad, longer than 2, with ventromedial acute process exceeding first third of first flagellar article; article 2 with similar process exceeding half of first flagellar article; article 3 shorter than flagellar article 1; accessory flagellum absent; flagellum consisting of three articles, article 1 longest with aesthetascs ventrally. Antenna 2 (Fig. 1d): subequal in length to antenna 1; article 2 with subacute gland cone; articles 2 and 3 subequal in length; article 4 with long acute medial process almost reaching distal margin of peduncular article 5; article 5 as long as flagellum; flagellum consisting of 3 articles.

Labrum (Fig. 1c): elongated, tapering distally; epistome forming keel-like process. Mandible (Fig. 2d, e): styliform; incisor simple, very small, with cutting edge, slender lacinia mobilis on left mandible, absent on right mandible; pars molaris small, cup-like weakly triturative; palp 3-articulate, article 1 slightly expanded distally, 0.82 as long as article 2, article 2 longest, article 3 0.91 as long as article 2, curved ventrally, with linear comb row, apically with 3 short setae. Hypopharynx (Fig. 2f): slender, long and narrow apices. Maxilla 1 (Fig. 2a): inner plate small, outer plate styliform with 5–6 spine-like setae distomedially; palp uniarticulate, short with long seta distally. Maxilla 2 (Fig. 2b); inner plate wider than outer plate with 8 setae distally; outer plate longer than inner plate with 10 setae distally. Maxilliped (Fig. 2c): inner plate slender, long (70% of outer plate), spine-like seta apically, row of setae on medial margin; outer plate rounded distally with several setae subapical; palp present, uniarticulate (remnants of former articular suture visible under high magnification), 1 long and 1 short inconspicuous setae terminally.

Gnathopod 1 (Figs. 1a, 3a): coxa much shorter than coxa of pereopod 2 (65%), tapering distally; basis elongate, slightly longer than ischium and merus together; carpus and propodus subequal in length and width; propodus with some setae distally; dactylus with some plumose setae and one stout seta posteriorly. Gnathopod 2 (Figs. 1a, 3b): coxa elongated, rounded distally, anteroproximal angle overlapping coxa 1; basis elongate, ischium shorter than merus; posterodistal angle of merus bearing process; carpus longer than propodus, increasing in width distally, with setae on posterodistal process; dactylus stout, bifid with claw anteriorly (see detail of Fig. 3b).

Pereopod 3 (Fig. 3c): anteroproximal part of coxa rounded, overlapping coxa 2, posteromarginal rounded process, coxa tapering distally to subacute tip; basis slightly increasing in width distally; ischium short and broad; merus with anterodistal acute process (carpus to dactylus missing). Pereopod 4 (Fig. 4a): coxa broad, anteriorly and posteriorly excavate, overlapping coxa 3 proximally; basis simple; merus similar in

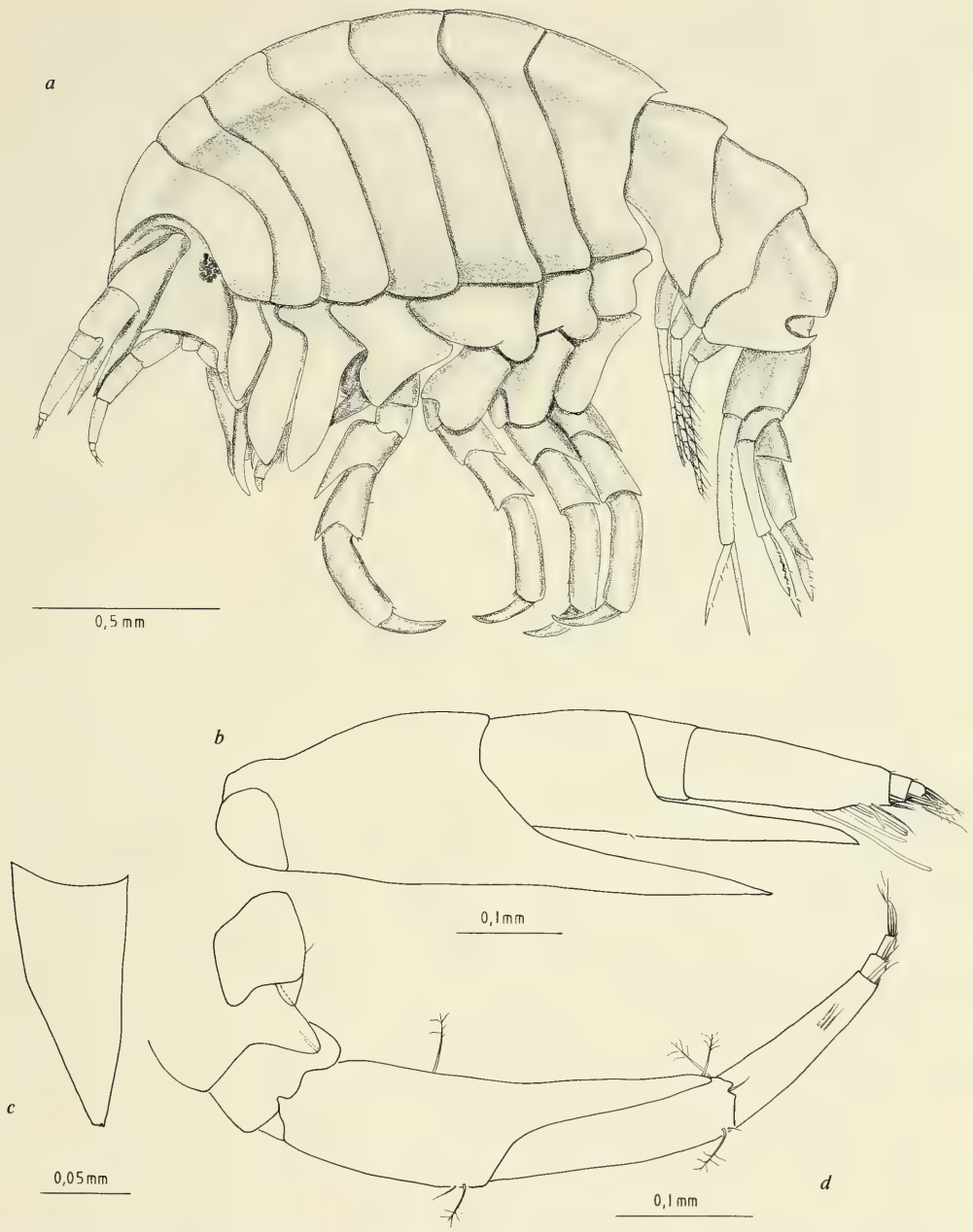


Fig. 1. Holotype of *Curidia magellanica* n. sp., female 2.4 mm. a, lateral habitus; b, antenna 1; c, labrum; d, antenna 2.

shape as to pereopod 3; carpus increasing in width distally with some spine-like setae posteromarginally, anterodistal angle slightly produced; propodus longer than merus, with some spine-like setae posteromarginally; dactylus stout with terminal claw. Pereopod 5 (Figs. 1a, 4e): coxa very broad, anteroproximal corner produced, overlapping coxa 4; basis broad with inconspicuous ridge on lateral face, overlapping

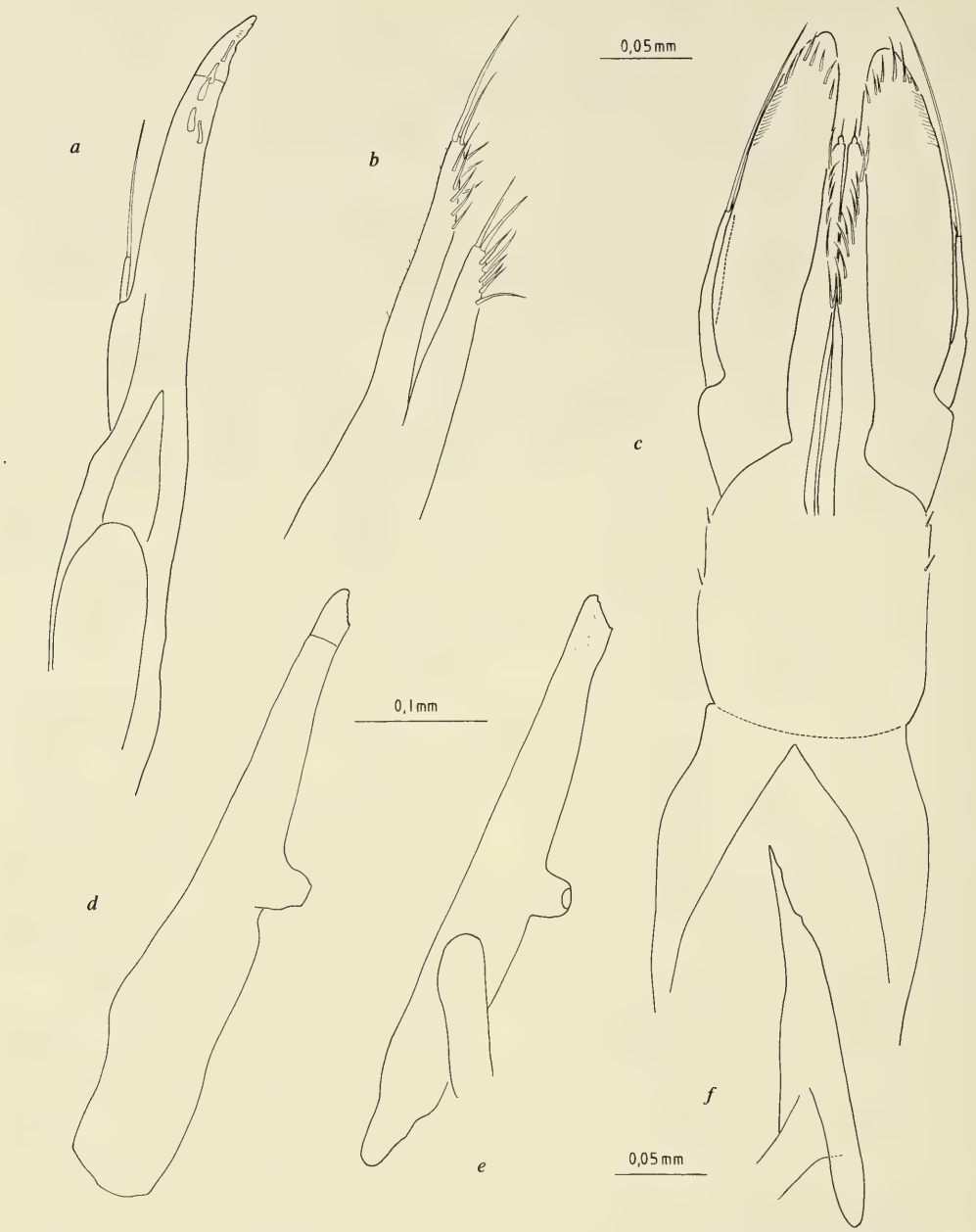


Fig. 2. Holotype of *Curidia magellanica* n. sp., female, 2.4 mm. a, maxilla 1; b, maxilla 2; c, maxilliped; d, left mandible; e, right mandible; f, part of hypopharynx.

ischium and merus with posterodistal lobe; merus broad with posterodistal process (carpus to dactylus damaged during dissection). Pereopod 6 (Figs. 1a, 4b): coxa broader than long, slightly excavate posteriorly, anteroproximally lobate; basis similar in shape to pereopod 5 but slightly longer, merus broad with acute posterodistal process; carpus longer than merus, increasing in width distally, posterodistal angle slightly

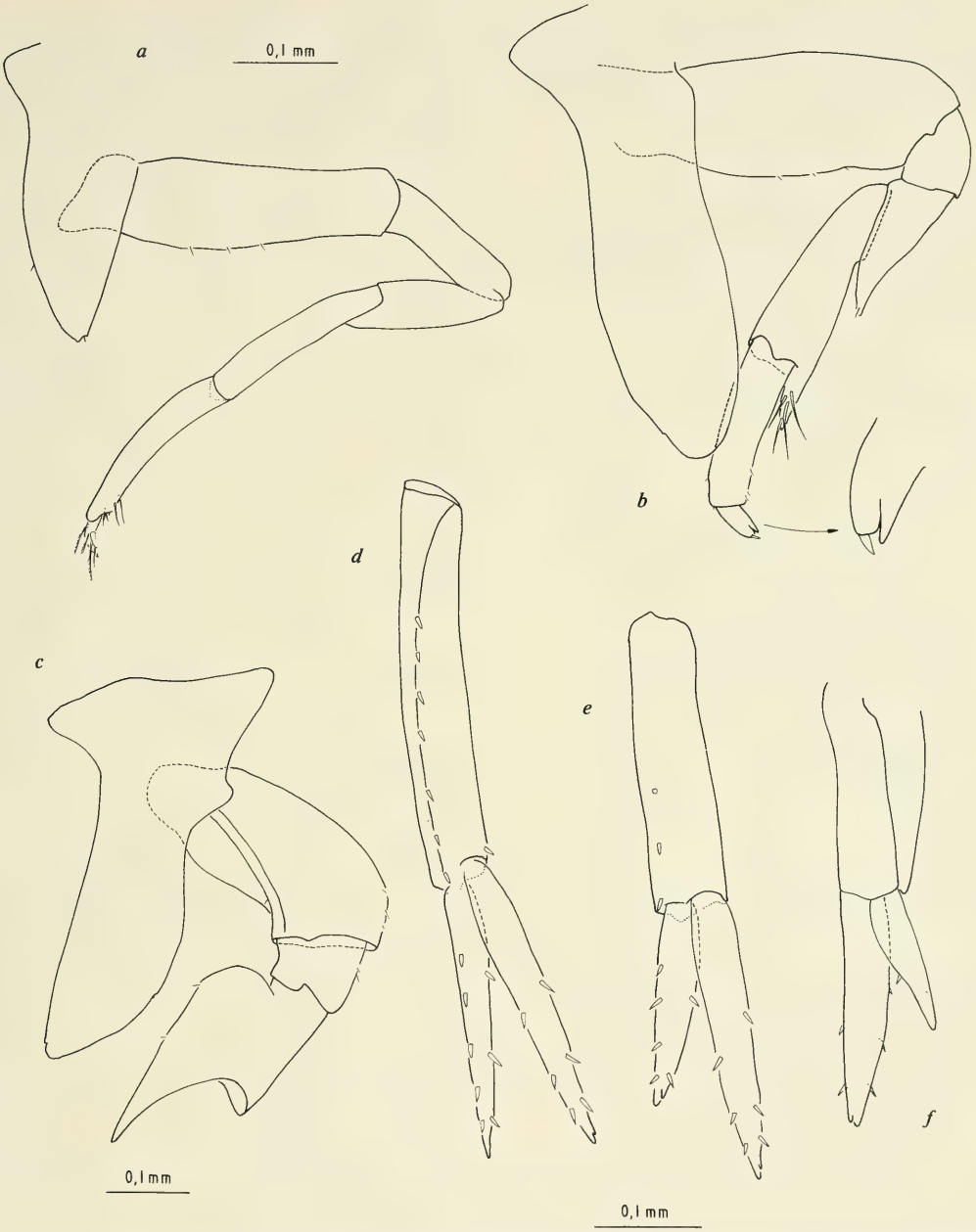


Fig. 3. Holotype of *Curidia magellanica* n. sp., female, 2.4 mm. a, pereopod 1; b, pereopod 2, detail showing dactylus with claw; c, pereopod 3; d, uropod 1; e, uropod 2; f, uropod 3, from ventral side.

produced; propodus longest with some spine-like setae anteromarginally; dactylus stout with terminal claw. Pereopod 7 (Figs. 1a, 4c): coxa small, with posteromarginal excavation; basis similar in shape to pereopods 5 and 6 but broader, anteromarginally sinuoid; ischium, merus, carpus and dactylus as for pereopod 6.

Gills present on coxae 2–7 slender, weakly sac-like but on pereopod 7 as long as

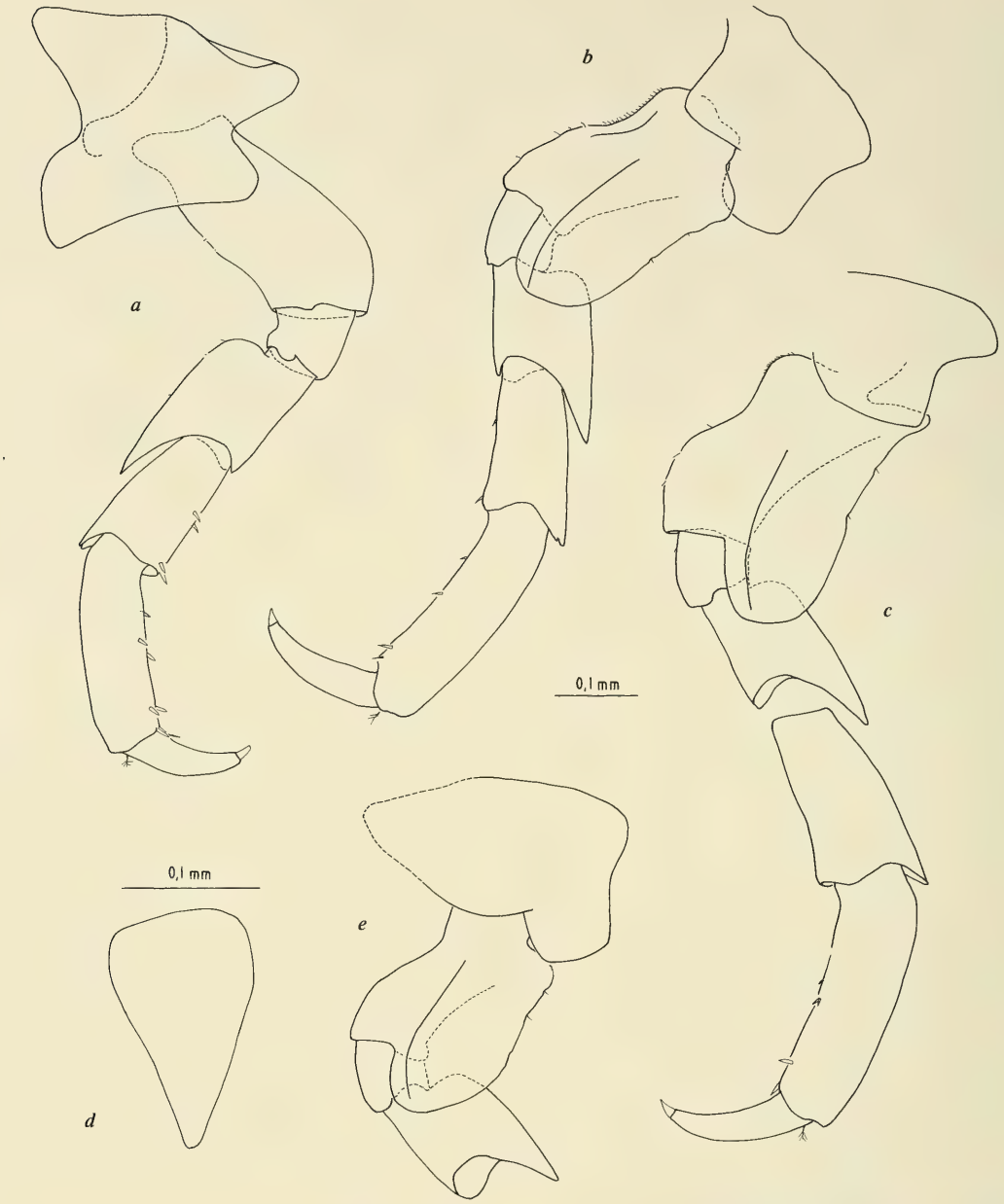


Fig. 4. Holotype of *Curidia magellanica* n. sp., female, 2.4 mm. a, pereopod 4; b, pereopod 6; c, pereopod 7; e, pereopod 5. Paratype, ovigerous female, 2.9 mm. d, telson.

broad. Oostegites on coxae 2–4 broadly expanded distally, rounded, oostegite of coxa 5 short and slender.

Uropod 1 (Figs. 1a, 3d): slightly reaching beyond uropods 2 and 3, peduncle elongate, longer than rami, with row of spiniform setae dorsolaterally; rami subequal in length, some spine-like setae on both margins. Uro-

pod 2 (Figs. 1a, 3e): peduncle subequal to inner ramus, length of outer ramus ⅔ of inner ramus, rami with spine-like setae on both margins. Uropod 3 (Figs. 1a, 3f): peduncle stout; inner ramus longer than outer ramus. Telson (Fig. 4d, from paratype): entire, elongate, tapering distally.

Descriptive note.—Because the mandibular palp and telson were damaged on the holotype, descriptions are taken from a paratype ovigerous female 2.9 mm.

Discussion.—The Ochlesidae consist of the apomorphic genera *Meraldia* Barnard & Karaman (1987) and *Ochlesis* Stebbing (1910) lacking a maxillipedal palp and the plesiomorphic genus *Curidia* Thomas (1983) with an uniarticulate palp. The plesiomorphic genus *Ochlesodius* Ledoyer (1982), bearing a 2-articulate maxillipedal palp, was placed with the Iphimediidae by Ledoyer (1982). This genus should be moved to the Ochlesidae, which seem to be related to the Iphimediidae (compare Bousfield 1978). Ledoyer (1986) points at the similarity between *Ochlesis* and *Odius,* an iphimediid "à laquelle ils [the ochlesids] pourraient être rattaches." On the contrary, Coleman & Barnard (1991) moved *Odius* to the new family Odiidae because it has more characters in common with the Ochlesidae and does not fit well in the Iphimediidae.

The new species is relegated to the genus *Curidia* owing to its uniarticulate maxillipedal palp by which it is separated from *Ochlesodius spinicornis* Ledoyer, 1982. Although the body shape of the new species is similar to *Curidia debrogania* and *Ochlesodius spinicornis,* the new species is clearly distinguished from those species by the strong development of the pointed projections in the peduncular articles 1 and 2 of antenna 1 and the fourth article of antenna 2. The coxal plates of pereopods 2 and 3 of *Ochlesodius spinicornis* are apically truncate, in *Curidia magellanica* rounded and subacute, respectively. The maxillipedal palp is much longer in the new species compared to *Curidia debrogania* and there are remnants of an articular suture, which might indicate relations to the genus *Ochlesodius.*

Literature Cited

Barnard, J. L. 1970. Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands.—Smithsonian Contributions to Zoology 34:1–286.

———. 1972. Gammaridean Amphipoda of Australia, Part I.—Smithsonian Contributions to Zoology 103:1–333.

———, & C. M. Barnard. 1983. Freshwater Amphipoda of the world, I. Evolutionary patterns and II. Handbook and bibliography. Mt. Vernon, Virginia, Hayfield Associates, xix + 830 pp.

———, & G. S. Karaman. 1987. Revisions in classification of gammaridean Amphipoda (Crustacea) Part. 3.—Proceedings of the Biological Society of Washington 100:856–875.

Barnard, K. H. 1940. Contributions to the crustacean fauna of South Africa. XII. Further additions to the Tanaidacea, Isopoda, and Amphipoda, together with keys for the identification of the hitherto recorded marine and fresh-water species.—Annals of the South African Museum 32: 381–543.

Bousfield, E. L. 1978. A revised classification and phylogeny of amphipod crustaceans.—Transactions of the Royal Society of Canada 4:343–390.

Coleman, C. O., & J. L. Barnard. 1991. Revision of Iphimediidae and similar families (Crustacea: Amphipoda).—Proceedings of the Biological Society of Washington 104:253–268.

Griffiths, C. L. 1974a. The Amphipoda of southern Africa part 2. The Gammaridea and Caprellidea of South West Africa south of 20°S.—Annals of the South African Museum 62:169–208.

———. 1974b. The Amphipoda of southern Africa part 3. The Gammaridea and Caprellidea of Natal.—Annals of the South African Museum 62: 209–264.

———. 1974c. The Amphipoda of southern Africa part 4. The Gammaridea and Caprellidea of the Cape Province east of Cape Agulhas.—Annals of the South African Museum 65:251–336.

———. 1975. The Amphipoda of southern Africa part 5. The Gammaridea and Caprellidea of the Cape Province west of Cape Agulhas.—Annals of the South African Museum 67:91–181.

Ledoyer, M. 1982. Crustacés amphipodes gammariens familles des Acanthonotozomatidae a Gammaridae.—Faune de Madagascar 59(1):1–598.

———. 1986. Crustacés amphipodes gammariens familles des Haustoriidae à Vitjazianidae.—Faune de Madagascar 59(2):599–1112.

Pirlot, J. M. 1936. Les amphipodes de l'expédition du Siboga. Deuxiéme partie. . . . II.-Les amphipodes de la mer profonde. III. Les amphipodes littoraux. 1. Lysianassidae. . . Gammaridae.—Siboga-Expéditie 33e:237–328.

Schellenberg, A. 1938. Litorale Amphipoden des tropischen Pazifiks.—Kunglia Svenska Vetenskapsakademiens Handlingar (3)16(6):1–105.

———. 1953. Erganzungen zur Amphipodenfauna Sudwest-Afrikas nebst Bemerkungen uber Brutraumbildung.—Mitteilungen aus dem Zoologischen Museum in Berlin 29:107–126.

Stebbing, T. R. R. 1910. Crustacea. Part V. Amphipoda. Scientific results trawling expedition H.M.C.S. "Thetis."—Australian Museum, Memoir 4, 2:565–658.

Thomas, J. D. 1983. *Curidia debrogania,* a new genus and species of amphipod (Crustacea: Ochlesidae) from the barrier reefs of Belize, Central America.—Proceedings of the Biological Society of Washington 96:127–133.

(COC) Fachbereich 7, Zoomorphologie, Universitat Oldenburg, Postfach 2503, D-2900, Oldenburg, F.R.G.; (JLB) NHB-163, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 279–287

AMATIGUAKIUS FORSBERGHI, A NEW GENUS AND SPECIES FROM ALASKA (MARINE AMPHIPODA: EPIMERIIDAE)

C. O. Coleman and J. L. Barnard

Abstract.—The new genus and species, *Amatiguakius forsberghi,* was collected in "pink coral" at 37 meters of depth from the Aleutian Islands. The new genus differs from other members of Acanthonotozomellidae in the prominent rounded lateral carinae, and laterally ridged dorsal carinae; the presence of 2 ridges on the broad dorsal carinae of pereonite 7 and pleonites; the extreme multispinosity of the outer plate on maxilla 1; the strong setation on the inner plate of maxilla 1; and, on antenna 2, the reduction of the flagellum to 3 articles, with antenna 2 shorter than antenna 1.

The new taxon, *Amatiguakius forsberghi,* to be described below, is the only species of its family found in the arctic-subarctic region; all other species occur in the antarctic-subantarctic region.

The difficulty in classifying this species was one of the reasons we (Coleman & Barnard 1991) undertook a revision of the genera in the old Epimeriidae and Iphimediidae. Part of that revision included the establishment of a new family, Acanthonotozomellidae, in which *Amatiguakius* is now placed. A key to the genera of the family is presented below and references to those genera may be found in Coleman & Barnard (1991).

Acanthonotozomellidae

Acanthonotozomellidae Coleman & Barnard, 1991:257.

Key to the Genera of Acanthonotozomellidae

1. Body processes bluntly rounded .. .. *Acanthonotozomopsis*
– Body processes acute or formed into distinctly dorsal carinae 2
2. Article 2 of maxillipedal palp medially produced . *Acanthonotozomoides*
– Article 2 of maxillipedal palp not produced 3
3. Pereonite 1 with 1 dorsal carina, coxae 2–3 divergent .... *Acanthonotozomella*
– Pereonite 1 with 2 dorsal carinae, coxae 2–3 similar ..... *Amatiguakius*

Amatiguakius, new genus

Diagnosis.—Body stout, with dorsal carinae on pereon and metasome; pereonite 1 with 2 dorsal carinae, dorsal carinae laterally ridged, carinae on pereonite 7 and metasomites wide, with 2 ridges; lateral carinae strongly produced and rounded; head short, with straight rostrum, lateral cephalic lobes rounded; antenna 2 shorter than 1; peduncle of antenna 1 stout, with acute processes; labrum with narrow notch; mandible with narrow incisor and setal row, but no molar; lacinia mobilis present on both mandibles; maxilla 1 with large inner plate, outer plate with numerous spiniform setae, palp exceeding outer plate; setae of maxilla 2 medioapically comb-like setulate; maxillipedal palp slender, article 2 not produced; coxae 1 to 3 pointed, similar in shape and ridged; gnathopods simple, similar; bases of pereopods 5 to 7 broad, lobate ventrally; pereopods 3–7 with small setae on medial and lateral surfaces; dactyli with spiniform setae on concave margin. Telson entire.

Relationship.—The new genus bears some

resemblance to the genus *Paramphithoe* Bruzelius, 1859, in the family Epimeriidae (= Paramphithoidae, compare with Gurjanova 1972), for example: two dorsal carinae on pereonite 1; strongly produced lateral carinae; acute coxae 1 to 3. On the other hand, the head of the new species lacks a pointed lateral cephalic lobe; a mandibular molar is absent; coxa 4 is not deeply excavate; the bases of pereopods 5–7 are lobate ventrally; and the telson is short and distally rounded.

On closer view, the new type species is similar to the "Acanthonotozoma-complex" (compare Watling & Holman 1980). In particular, *Acanthonotozomella* Schellenberg, 1926, *Acanthonotozomopsis* Watling & Holman, 1980, and *Acanthonotozomoides* Schellenberg, 1931 seem to be closely related; these genera have been relegated to a new family Acanthonotozomellidae by Coleman & Barnard (1991). The combination of characters typical of *Acanthonotozomella, Acanthonotozomopsis, Acanthonotozomoides* and *Amatiguakius* that differs from genera in the Iphimediidae is as follows: gnathopods simple, similar in shape and setation (versus differences in lengths, setation and the typical euchela found in all true iphimediids); and setal raker row present (absent in Iphimediidae). The genera mentioned above bear in common: body dorsally armamented; lateral carinae present; labrum narrowly notched; mandibles with raker row, molar absent; lobes of maxilla 2 with similar setae; short and rounded telson; and dactyli at least of gnathopods with spiniform setae on concave margin. *Acanthonotozomella barnardi* Watling & Holman, 1980 and the new species bear setae in the hypopharyngeal gap. The rostra of *Acanthonotozomoides sublitoralis, Acanthonotozomella barnardi, Acanthonotozomella alata* and the new species have raised lateral edges.

The Acanthonotozomellidae differ from the monotypic Acanthonotozomatidae in the presence of mandibular rakers.

The Acanthonotozomellidae differ from the Amathillopsidae in the absence of a molar, feeble gnathopods, and lack of inner lobes on the lower lip.

The erection of the new genus was necessary because of the remarkable differences from the known genera of Acanthonotozomellidae: the prominent rounded lateral carinae; the laterally ridged dorsal carinae; the presence of 2 ridges on the wide dorsal carinae of pereonite 7 and pleonites; antenna 2 with 3 flagellar articles; and antenna 2 shorter than antenna 1.

Amatiguakius forsberghi, new species
Figs. 1–5

Etymology.—The generic name refers to the type locality. The species name is derived from the collector of the material.

Holotype.—USNM 253545, female, 28 mm in length, with setose oostegites.

Type locality.—East side of Amatiguak Island, Aleutian Islands; 13 Jul 1958; collected by Eric D. Forsbergh (Inter-American Tropical Tuna Commission) "on pink coral, caught on . . . line" [fishing line?]; depth, 20 fathoms.

Description.—Body: Stout, pereonites and pleonites with dorsal carinae, laterally ridged as in Fig. 1b. Lateral carinae on pereonites strongly projecting as in Fig. 1a. Pereonite 1 with 2 dorsal carinae, anterior carina shorter, pointing anteriorly, posterior carina slightly bent posteriorly, similar in shape and length to carinae of succeeding segments; dorsal carinae of pereonite 7 and metasome with 2 ridges laterally and wider than preceding segments (seen from lateral view); metasomal epimera ridged as in Fig. 1b, with acute process posterolateromarginally; urosomite 1 longest, with middorsal acute process, short posteromarginal process on urosomite 2, urosomite 3 excavate posteromarginally.

Head (Fig. 1c, d): Short (about as long as pereonites 1–2 together, partially hidden under coxa 1; with weak posterior elevation

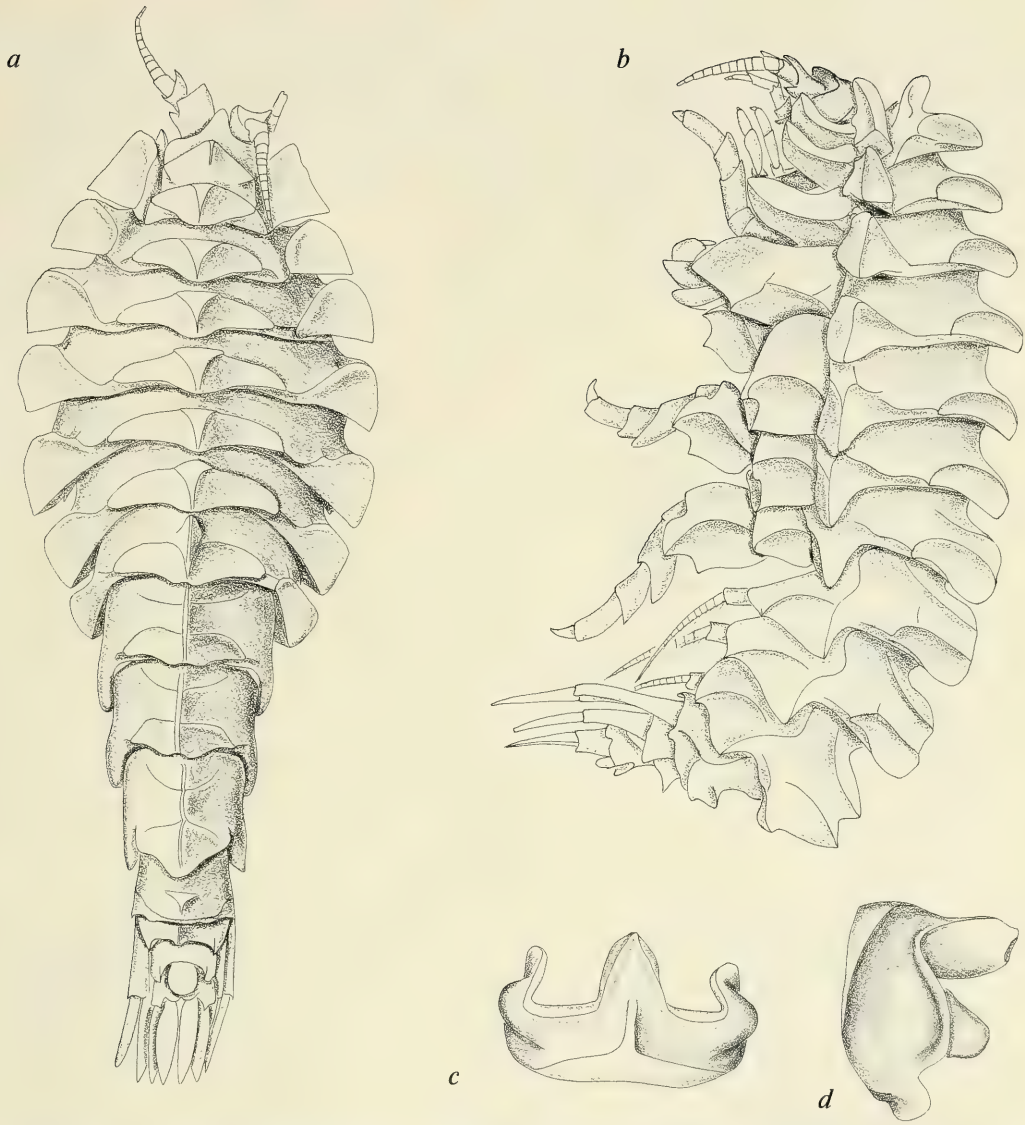


Fig. 1. a–d. *Amatiguakius forsberghi* n. sp., holotype, 28 mm in length. a, dorsal view, b, lateral view, c, head seen from dorsal, d, right lateral side of head.

and dorsal ridge; horizontal rostrum with raised lateral edges, truncate anteriorly in lateral view; rounded epistomal process between antennae 2, round lateral bulges, but no ommatidia or pigmentation (blind?); ventrolateral lobes rounded, slightly bent laterally.

Antenna 1 (Fig. 2a): Short, peduncular article 1 stout, with pointed process laterally; article 2 shorter, with acute process; article 3 shortest; two small rounded projections medially and proximally to flagellum, smaller one with two setae distally (vestigial accessory flagellum?); flagellum with 11 articles, each with conspicuous group of long aesthetascs and setae apically (Fig. 2c). Antenna 2 (Fig. 2b).—Shorter than antenna 1 (about 55%); peduncular articles

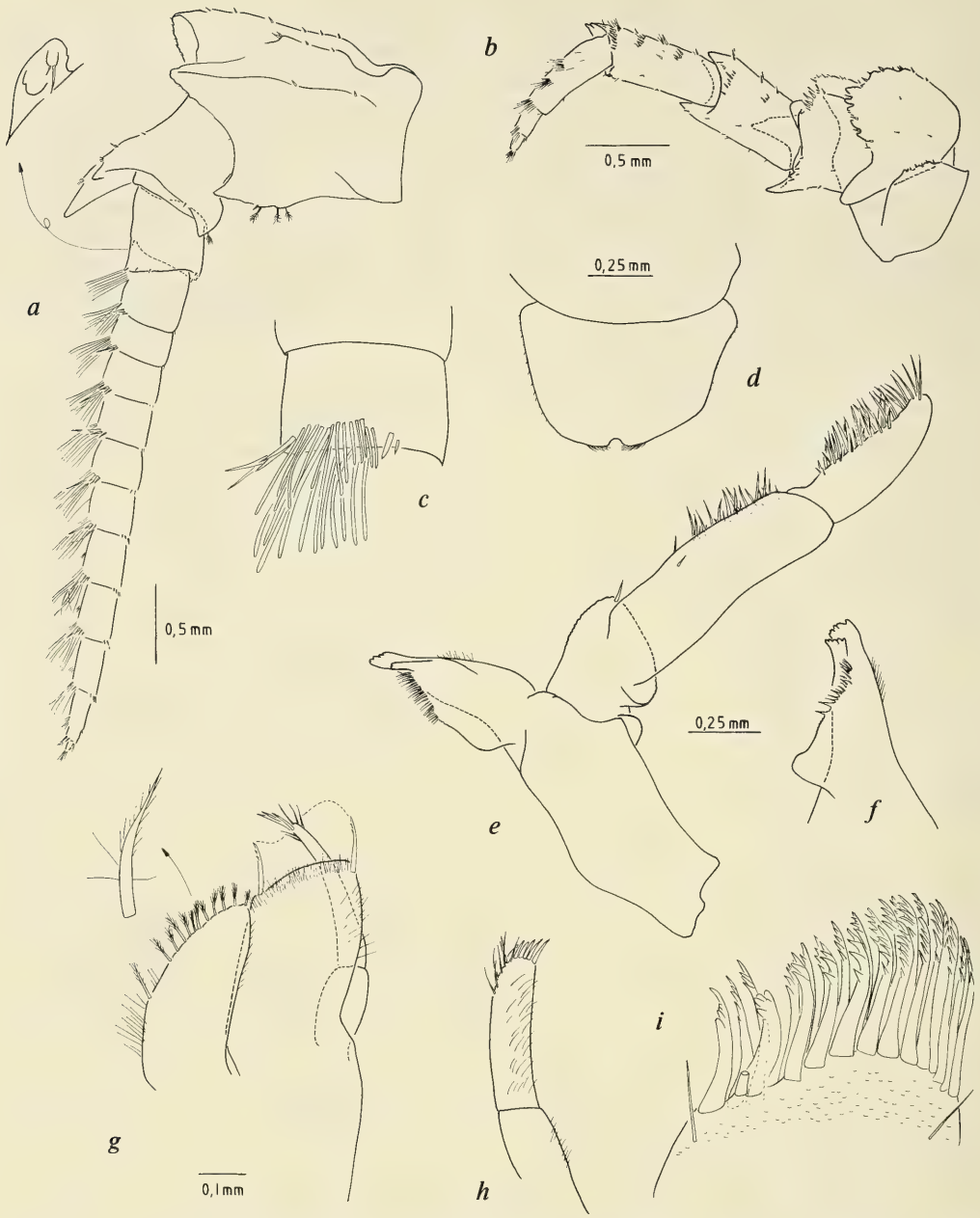


Fig. 2. a–l. *Amatiguakius forsberghi* n. sp., holotype, 28 mm in length. a, antenna 1, b, antenna 2, c, detail of antenna 1, d, labrum, e, right mandible, f, distal part of left mandible, g, maxilla 1, setae on outer plate omitted, dotted line indicates length of spiniform setae, h, palp of maxilla 1, i, spiniform setae on outer plate of maxilla 1, place of insertion of hair-like setae is shown.

1–3 short, distally serrate with short setae, articles 4–5 subequal in length, covered with groups of short setae; flagellum 3-articulate, article 1 longest, with 3 groups of setae.

Labrum (Fig. 2d): Ventral margin rounded, medially notched.

Mandibles (Fig. 2e, f): Slender, incisors narrow, weakly toothed; right mandible with

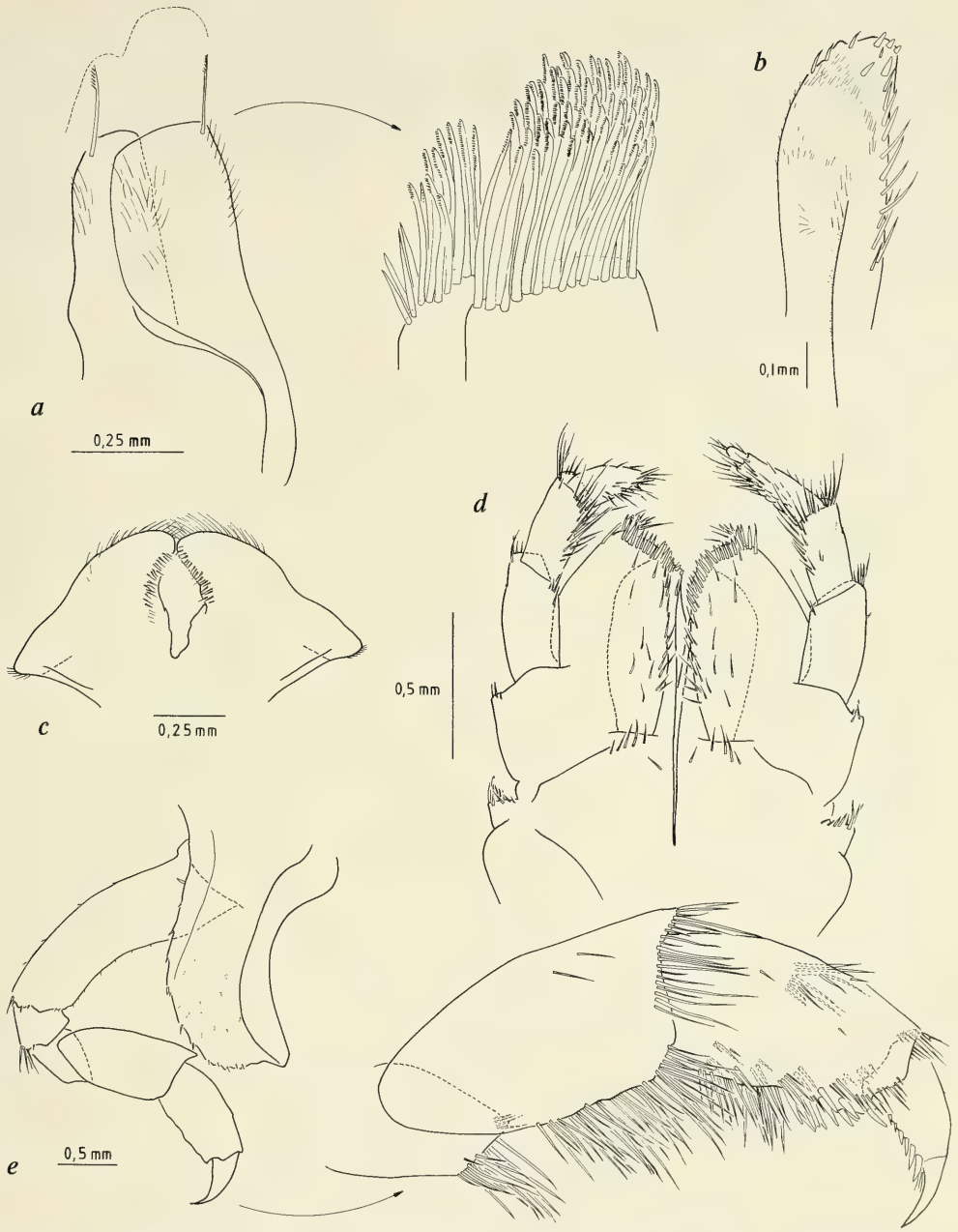


Fig. 3. a–e. *Amatiguakius forsberghi* n. sp., holotype, 28 mm in length. a, maxilla 2, dotted line indicates lengths of setae, detail shows apical region of inner and outer plate, b, inner plate of maxilliped, seen from oral side, c, lower lip, d, maxilliped, seen from ventral side, e, pereopod 1, setation of merus to dactylus on detail.

slender lacinia mobilis, left lacinia broader (Fig. 2f); raker setal row on thin projecting lamella, molar absent; palp 3-articulate, article 2 longest, with setae ventrally, article 3 slightly bent laterally, densely setose ventrally.

Lower lip (Fig. 3c): Broad; apices rounded, bent medially, covered with hair-like

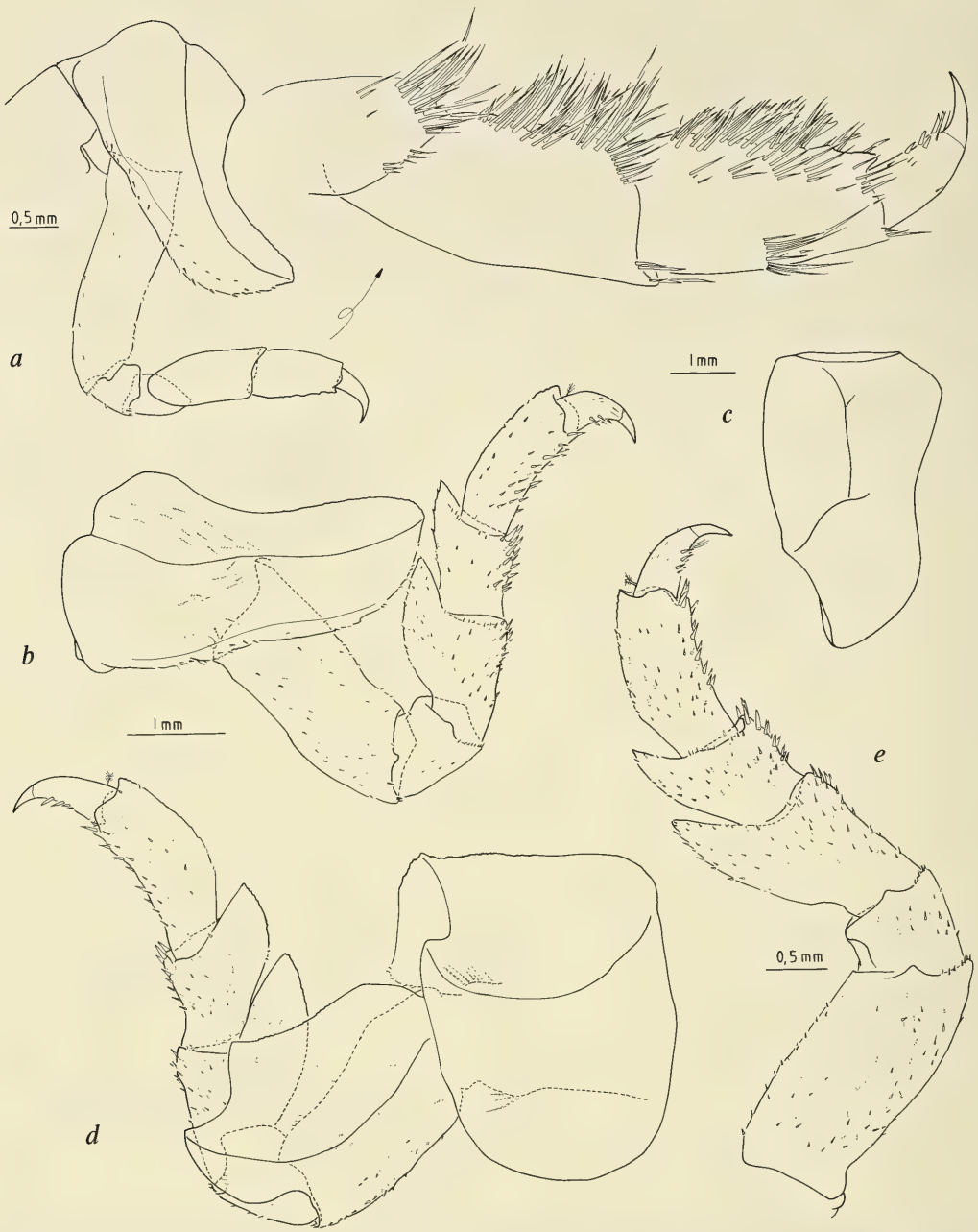


Fig. 4. a–e. *Amatiguakius forsberghi* n. sp., holotype, 28 mm in length. a, pereopod 2, setation of merus to dactylus shown on detail, b, pereopod 3, c, coxa of pereopod 4, d, pereopod 5, e, pereopod 4.

setae apically; hypopharyngeal gap with setae medially; mandibular processes broad, with hair-like setae posteriorly.

Maxilla 1 (Fig. 2g–i): Inner plate relatively large, with 12 setulated setae mediomarginally; outer plate broad, densely covered with hair-like scales apically, with numerous (29?) spine-like setae, each ser-

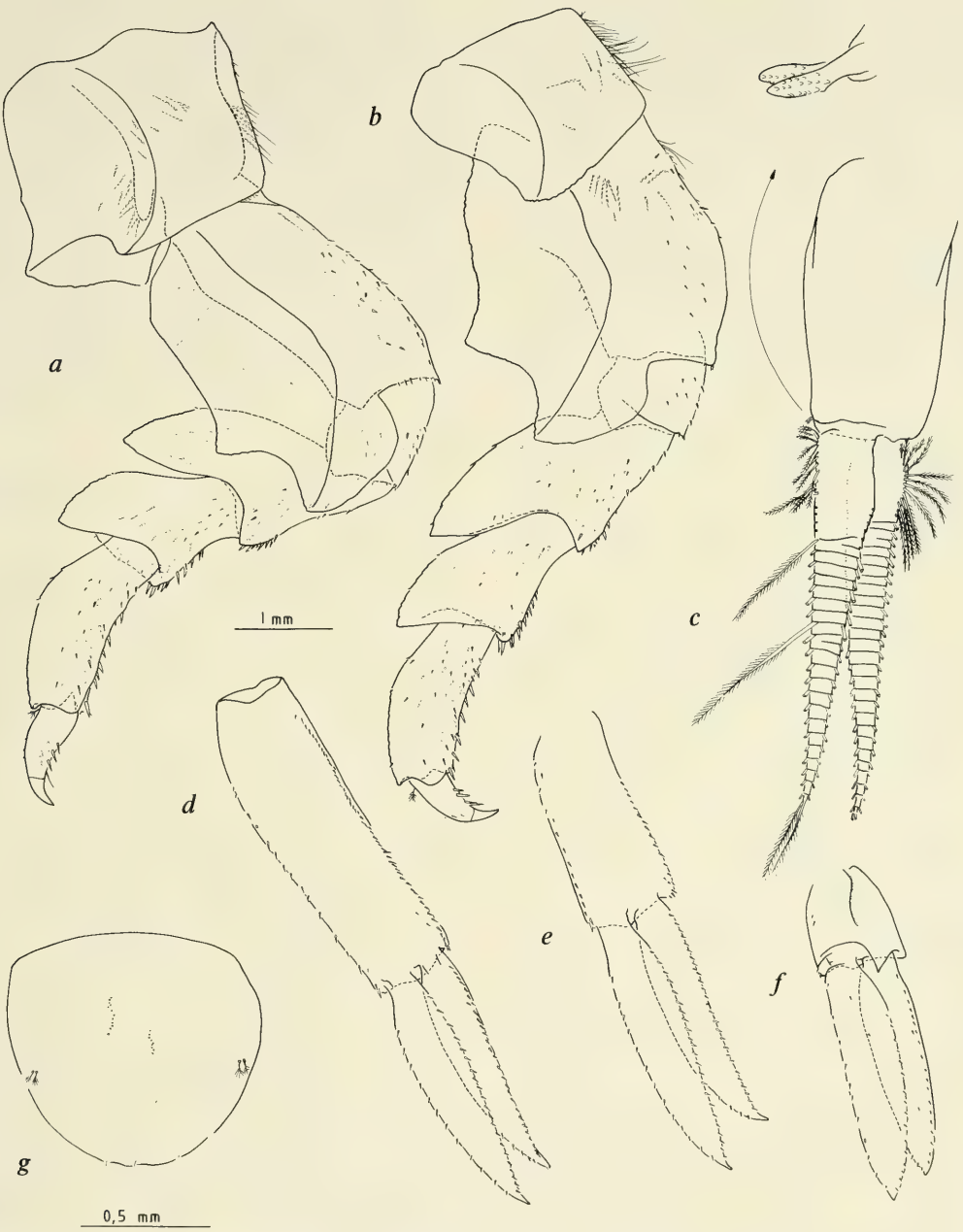


Fig. 5. a–g. *Amatiguakius forsberghi* n. sp., holotype, 28 mm in length. a, pereopod 6, b, pereopod 7, c, pleopod 1, detail shows coupling hooks, d, uropod 1, e, uropod 2, f, uropod 3, g, telson.

rate medioapically (Fig. 2i); slender palp 2-articulate, exceeding outer plate, stout setae apically, slender setae laterally.

Maxilla 2 (Fig. 3a): Outer plate wider than inner plate, equal in length, very dense setation especially on outer plate, all setae distomedial comb-like setulate (except short medial straw-like scales on face of inner plate).

Maxilliped (Fig. 3b, d): Inner plate elon-

gate, short spiniform setae on distomedial angle, smooth setae on medial margin, scales on oral face; outer plate broad, with spiniform setae apically, setae mediomarginally and on ventral face; palp relatively slender, 3-articulate on right, seemingly 4-articulate on left.

Gnathopod 1 (Fig. 3e): Coxa apically pointed, sinuoid anteriorly, ridged on lateral face, additional but weaker ridge near posterior margin, short setae posteromarginally; basis slender; ischium short; merus short with group of setae apically; carpus slightly expanded distally, densely covered with setae posteriorly and apically; propodus shorter than carpus (82%), with medial and posterior setation, spiniform setae distoventrally; dactylus with spiniform setae posteromarginally.

Gnathopod 2 (Fig. 4a): Coxa similar to coxa 1; basis, ischium and merus similar to gnathopod 1; carpus only slightly expanded distally, with posterior setation; propodus setose medially and posteriorly; dactylus spiniform, with slender setae posteriorly.

Pereopods 3–7: Lateral and medial faces of articles 2–7 covered with short setae.

Pereopod 3 (Fig. 4b): Coxa longer but similar in shape to preceding coxae, but not as excavate anteriorly, basis longer than ischium and merus; merus and carpus expanded distally, with process anterodistally, with spiniform setae posteromarginally; propodus slender, with spiniform setae posteromarginally; dactylus curved with spiniform setae and claw.

Pereopod 4 (Fig. 4c, e): Coxa ridged, elongated, sinuoid anteriorly and posterodistally; basis to dactylus similar to those of pereopod 3.

Pereopods 5–7: Similar except for coxae.

Pereopod 5 (Fig. 4d): Coxa ridged, wider than long, rounded anteriorly, with rounded process on coxal face posteroventrally; basis broad, longer than merus plus carpus, ridged, posteromarginal excavation bounded dorsally by triangular projection, lobate ventrally, covering ischium and merus partially; merus and carpus stout, expanded distally into posterodistal processes, spiniform setae anteromarginally; propodus slightly rounded posteriorly, spiniform setae anteromarginally, subequal in length to merus plus carpus; dactylus with spiniform setae anteriorly.

Pereopod 6 (Fig. 5a): Coxa subquadrate, with similar rounded process as on coxa 5; basis slightly longer than that of pereopod 5; ischium to dactylus as for pereopod 5.

Pereopod 7 (Fig. 5b): Coxa small, ridged; basis similar to that of pereopod 6, but slightly wider; ischium to dactylus as for pereopods 5 and 6.

Pleopod 1 (Fig. 5c): Peduncle rectangular; rami subequal; two coupling hooks as in detail of Fig. 5c.

Uropod 1 (Fig. 5d): Peduncle elongate, with numerous spiniform setae on both margins; rami shorter (0.8) than peduncle, outer ramus slightly shorter than inner ramus, rami with rows of spiniform setae on both margins.

Uropod 2 (Fig. 5e): Rami similar to those of uropod 1 but as long as peduncle.

Uropod 3 (Fig. 5f): Peduncle short, with dorsal process apically; rami lanceolate, about 2.5 times as long as peduncle, outer ramus slightly shortened, both rami with spiniform setae on both margins.

Telson (Fig. 5g): Distally rounded; two plumose setae on each side.

Discussion.—The asymmetrical development of the maxillipedal palp of the unique specimen of the new species may be due to loss and regeneration of the right palp. It is not clear if the rounded processes proximal to the flagellum of antenna 1 may be distinguished as remnants of an accessory flagellum.

Literature Cited

Bruzelius, R. M. 1859. Bidrag till kannedomen om skandinaviens Amphipoda Gammaridea.—Kongliga Svenska Vetenskaps-Akademiens Handlingar, new series, 3:1–104.

Coleman, C. O., & J. L. Barnard. 1991. Revision of

Iphimediidae and similar families (Amphipoda: Gammaridea).—Proceedings of the Biological Society of Washington 104:253–268.

Gurjanova, E. 1972. Novye vidy bokoplavov (Amphipoda, Gammaridea) iz severozapadnoi chasti Tikhogo Okeana.—Akademiia Nauk SSSR, Trudy Zoologicheskogo Instituta 52:129–200.

Schellenberg, A. 1926. Die Gammariden der deutschen Südpolar-Expedition 1901–1903.—Deutsche Südpolar-Expedition 18:235–414.

———. 1931. Gammariden und Caprelliden des Magellangebietes, Südgeorgiens und der Westantarktis.—Further Zoological Results of the Swedish Antarctic Expedition 1901–1903 2(6):1–290.

Watling, L., & H. Holman. 1980. New Amphipoda from the Southern Ocean, with partial revisions of the Acanthonotozomatidae and Paramphithoidae.—Proceedings of the Biological Society of Washington 93:609–654.

(COC) Fachbereich 7, Zoomorphologie, Universitat Oldenburg, Postfach 2503, D-2900, Oldenburg, F.R.G.; (JLB) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 288–294

A NEW GENUS AND TWO NEW SPECIES OF FRESHWATER CRABS FROM MÉXICO, *ODONTOTHELPHUSA TONINAE* AND *STYGOTHELPHUSA LOPEZFORMENTI* (CRUSTACEA: BRACHYURA: PSEUDOTHELPHUSIDAE)

Fernando Alvarez and José Luis Villalobos

Abstract.—*Odontothelphusa toninae* is described from the State of Chiapas. This is the third species of the genus *Odontothelphusa,* extending its range to the south and east. *Stygothelphusa lopezformenti,* a new genus and species, is described from northern Oaxaca, and is a cave-dwelling species with advanced modifications for a troglobitic life.

With the new species described in this paper, and others recently published (Alvarez 1989, Rodríguez & Hobbs 1989), the Isthmus of Tehuantepec appears, potentially, as the geographical area with the highest diversity of pseudothelphusid crabs. *Odontothelphusa toninae,* new species, is the third known species of the genus and it is probably the most primitive one, being the most similar to the *Potamocarcinus* line. *Stygothelphusa lopezformenti,* new species, is a cave-dwelling species which is highly modified from the typical pseudothelphusid body plan. Although it does not appear as specialized as the species of the genus *Typhlopseudothelphusa* Rioja, 1952, this new species is in a very advanced stage of adaptation to the cave environment, suggesting an established troglobitic life style. A comparison of the lengthening of appendages is presented between *Typhlopseudothelphusa* and *Stygothelphusa,* new genus, using the same ratios used by Rodríguez & Hobbs (1989). All the specimens are deposited in the Carcinological Collection, Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM). The gonopod terminology used is that proposed by Smalley (1964) and by Smalley & Adkison (1984). Carapace breadth and carapace length are abbreviated as cb and cl; catalog numbers are preceded by the letters EM which denote an access number; and the abbreviation USNM is for the Smithsonian Institution, National Museum of Natural History, Washington, D.C.

Odontothelphusa Rodríguez, 1982

Remarks.—This genus was proposed by Rodríguez (1982) for a species treated by Pretzmann (1968) as *Potamocarcinus* (*Zilchia*) *maxillipes* (Rathbun, 1898). The character that justified *Odontothelphusa* was the distinctly flattened apical part of the male gonopod with two spines on the mesodistal angle; one larger, strong spine on the mesoproximal angle, and a simple marginal process that does not reach the apex of the gonopod. In contrast, the genus *Potamocarcinus* exhibits a large triangular cephalic tooth and one or two smaller cephalic teeth, the apex of the gonopod is not flattened along a caudocephalic axis, and the marginal process is recurved over the apex. Recently, Rodríguez & Hobbs (1989) described *O. monodontis* from Grutas del Coconá in the State of Tabasco, México, which became the second species in the genus.

Odontothelphusa toninae, new species
Fig. 1

Holotype.—♂, cb 56.4 mm, cl 37.2 mm; small stream passing through the ruins of

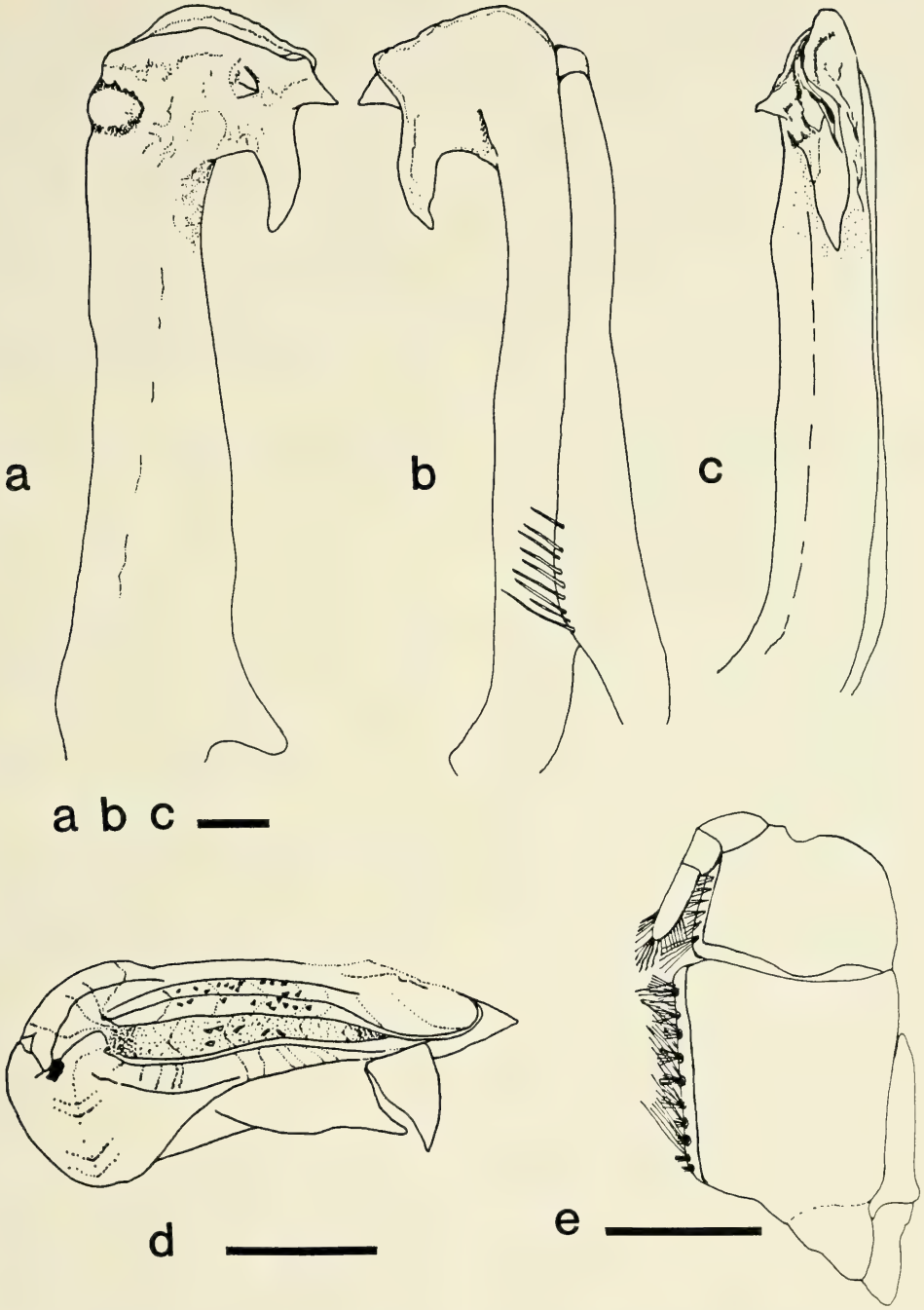


Fig. 1. Left gonopod and left third maxilliped of *Odontothelphusa toninae,* new species: a, lateral view; b, mesial view; c, cephalic view; d, apical view; e, left third maxilliped, outer view. Scale bars: a–d = 1 mm; e = 5 mm.

Toniná, Municipio de Ocosingo, Chiapas (16°53′N, 92°00′W), 8 Apr 1986, colls.: J. L. Villalobos, A. Cantú, and J. C. Nates; IBUNAM EM-7912.

Material examined.—7 ♂ (juveniles), cb 26.1, 25.8, 25.6, 23.1, 18.5, 14.4, 14.4 mm, cl 17.8, 17.5, 17.7, 15.9, 12.8, 10.6, 10.2 mm; 1 ♀, cb 33.4 mm, cl 22.4 mm; same locality and collectors as holotype; IBUNAM EM-7912A. 2 ♂, cb 34.7, 30.3 mm, cl 22.8, 20.6 mm; 4 ♀, cb 47.6, 25.7, 25.3, 20.9 mm, cl 31.2, 17.2, 17.1, 14.5 mm; highway Ocosingo-Palenque km 125, Chiapas (17°01′N, 92°08′W), 9 Apr 1986, colls.: D. Valle and E. Lira, IBUNAM EM-5770.

Description.—Carapace slightly convex. Frontal borders well marked; superior one straight, divided by median groove, inferior one continuous, bilobed in frontal view. Median groove deep and narrow. Postfrontal lobes present as two small elevations. Cervical grooves straight. Notch on anterolateral margin between orbit and cervical groove. Metagastric region limited by lateral depressions. Cardiac and intestinal regions discernible. Merus of third maxilliped with rounded notch on superior margin. Major chela on right side; dactyl teeth decreasing in size distally, propodus with two larger teeth in middle portion. Fingers leaving gap proximally.

Gonopod strong, straight. Large proximomesial spine oriented proximally, creating a hook-like shape. Superior margin of mesial crest straight, rounded caudally, forming a right angle cephalically. Distomesial spine triangular. Conical spine on cephalic surface. Rounded hump on caudal portion of lateral surface. Marginal process straight, short.

Etymology.—The specific name is derived from the Mayan ruins of Toniná, Chiapas, where the species occurs.

Remarks.—Similar to the species of the genus *Pseudothelphusa,* which display a progressive modification of lobes or processes of the male gonopod along a geographic gradient (Alvarez 1989, Rodríguez 1987). The species of *Odontothelphusa* also seem to fit this pattern, being distributed on an east–west axis, from the highlands of Chiapas to the Los Tuxtlas region in Veracruz. The species exhibit a rearrangement of the proximomesial spine towards the west. In addition, *O. monodontis,* occurring west of the range of *O. toninae,* shows a very reduced distomesial spine. *Odontothelphusa toninae* may be the most primitive species of the genus considering that it occurs in the southeastern limit of the range of the genus, and it shows the three cephalic spines that appear in *Potamocarcinus,* from which *Odontothelphusa* may be derived (Rodríguez 1982).

Stygothelphusa, new genus

Diagnosis.—Carapace convex, dorsal surface roughly divided into three regions: one cephalic and two branchial. Width of carapace 1.86 times its length. Front with 2 borders; superior one smooth, bilobed in dorsal view, divided into 2 distinct borders by wide median division; inferior one continuous. Postfrontal lobes present as two small elevations on carapace, distinct depression between gastric and cardiac regions. Cervical grooves straight, wide, shallow, not reaching anterolateral margin of carapace. Forty-four blunt denticles along anterolateral margin between orbit and posterior branchial region. Dorsal margin of orbit with internal section smooth, outer portion with 14 denticles. Shape of orbit atypical, elongated. Eyes complete, cornea pigmented. Third pair of walking legs 1.41 times width of carapace. Merus of third pereiopod 6.82 times as long as broad. Ratios of segments of walking legs as follows: carpus/merus 0.38, propodus/merus 0.60, and dactyl/merus 0.62. Ratio ischium/exopod of third maxilliped 0.37; merus with external margin rounded, internal margin straight. Pterygostomian region covered with setae. Major chela on right side. Merus of cheliped subtriangular in cross section, external mar-

Table 1.—Comparison of some ratios of troglobitic species of the genera *Typhlopseudothelphusa* Rioja, 1952, and *Stygothelphusa,* new genus.

Ratio	*T. hyba*[1]	*T. acanthochela*[2]	*T. mociñoi*[3]	*S. lopezformenti*
Carapace breadth/carapace length	1.46	1.53	1.58	1.86
3rd pereiopod length/carapace breadth	1.60	2.22	1.66	1.41
Segments of 3rd pereiopod				
Carpus/merus	0.35	0.34	0.38	0.38
Propodus/merus	0.66	0.68	0.69	0.60
Dactyl/merus	0.74	0.53	0.57	0.62

[1] Rodríguez & Hobbs (1989).
[2] Holotype (USNM 216239).
[3] Paratype (USNM 93740).

gin with tiny tubercles, internal and inferior margins with well defined spines of uniform size. Interior margin of carpus with typical large spine and 4 smaller spines proximally. Palm of right chela smooth, with distinct ridge on superior margin bearing small granules and spines; inferior margin similar to superior margin. Fingers gaping, dactyl with large proximal tooth, one small tooth proximal to large tooth, 10 small teeth distal to large tooth. Propodus with alternate large and small teeth. Propodus and dactyl slightly curved mesially, covered with small tubercles and spines forming 8 discernible longitudinal rows. For a comparison of ratios between *Stygothelphusa,* new genus, and *Typhlopseudothelphusa,* see Table 1.

Type species.—*Stygothelphusa lopezformenti,* new species.

Etymology.—The generic name is derived from the Latin "stygo" (subterranean waters) and "thelphusa," generic name for freshwater crabs.

Stygothelphusa lopezformenti, new species
Figs. 2, 3

Holotype.—♂, cb 47.2 mm, cl 25.6 mm; Cueva del Brujo, Rancho el Guayabo, 4 km south of Jacatepec, Municipio Valle Nacional, Oaxaca, 8 Oct 1968, coll.: W. López-Forment; IBUNAM EM-10034.

Description.—Gonopod straight and strong. In cephalic view, proximal ⅔ of gonopod twice as thich as distal ⅓. Mesial process semicircular in mesial view, with proximal field of spines; subtriangular in caudal view. In lateral view, gonopod uniformly broad with mesial process protruding distally. Lateral surface with 3 strong spines coming out from lateral crest. Marginal process simple, straight, reaching apex. In apical view, mesial process very prominent, slightly curved laterally, apex cavity elongated, field of setae in cephalic portion, field of small spines in caudal portion.

Etymology.—The species name is derived from the collector's name William López-Forment.

Remarks.—A new genus is proposed due to the unique body proportions found in this crab and to the distinct gonopod morphology. This genus is placed in the Tribe Potamocarcinini based on the following characters: straight gonopod with elongated apical field of spines, and a very large mesial spine [equivalent to the "strong triangular tooth" defined by Rodríguez (1982)]. In posterior view, there are similarities among the gonopods of *S. lopezformenti* and *Potamocarcinus richmondi, P. magnus, P. aspoekorum,* and *P. leptomelus,* namely the position of the marginal process and appearance of mesial process. However, the gonopod's apex is not *Potamocarcinus*-like, resembling more the typical *Pseudothelphusa* morphology. The pereiopods of *S. lopezformenti* are intermediate between those

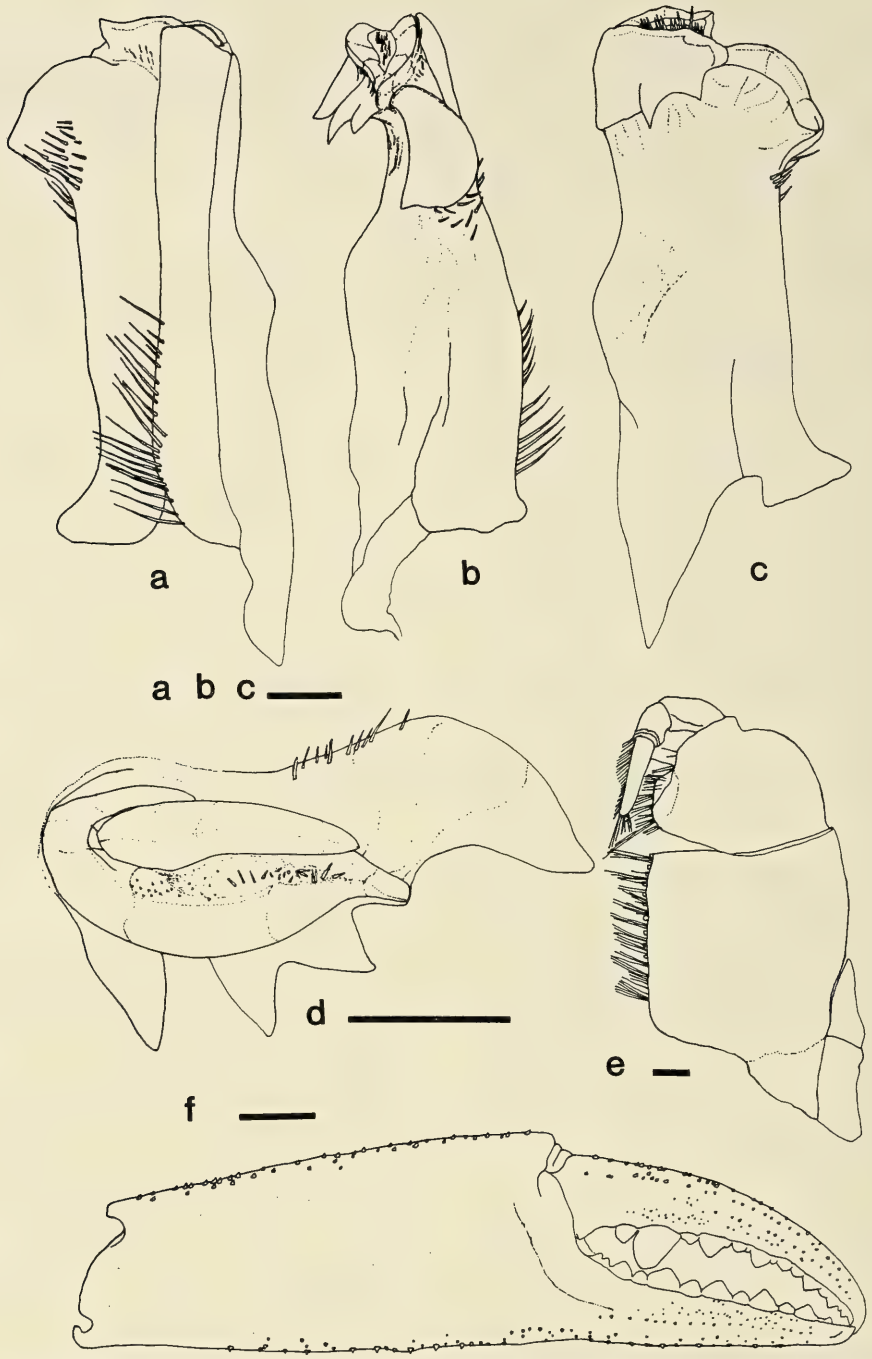


Fig. 2. Left gonopod, left third maxilliped, and major chela of *Stygothelphusa lopezformenti,* new species: a, mesial view; b, cephalic view; c, lateral view; d, apical view; e, left third maxilliped; f, right chela, outer view. Scale bars: a–e = 1 mm; f = 5 mm.

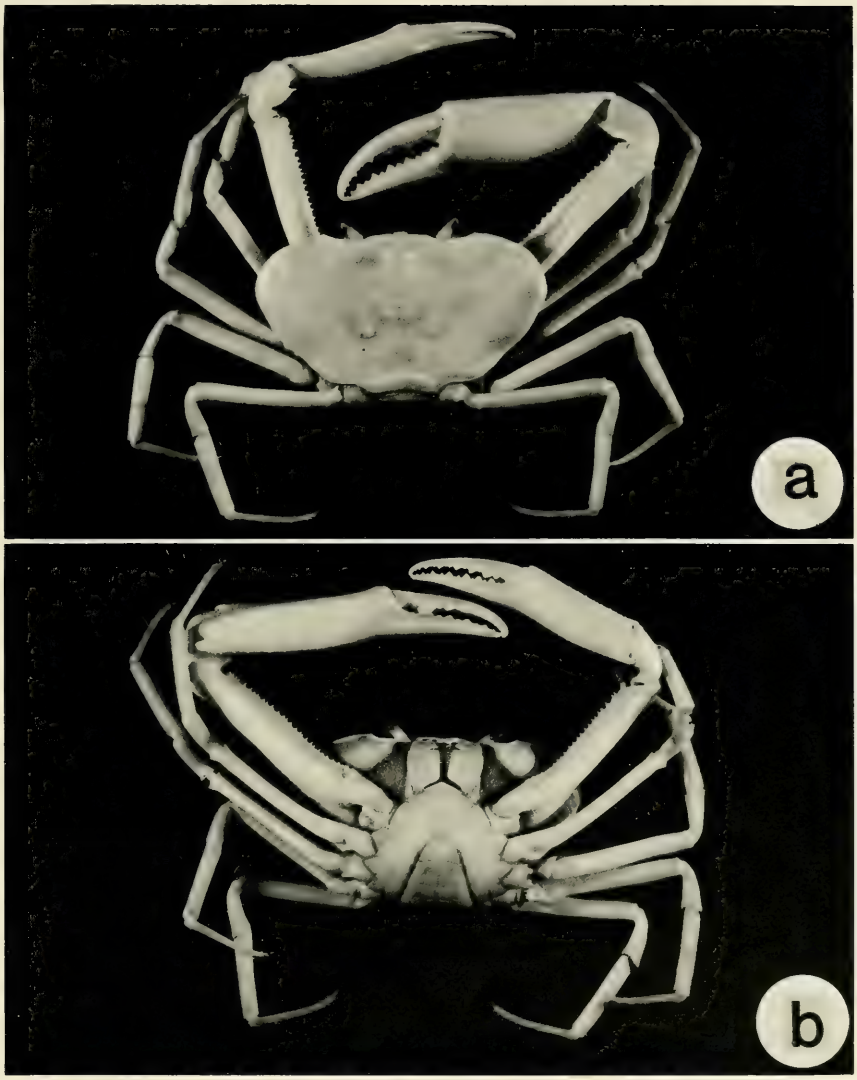


Fig. 3. *Stygothelphusa lopezformenti,* new species. Holotype (cb 47.2 mm): a, dorsal view; b, ventral view.

of the genus *Typhlopseudothelphusa* and those of epigean species. The carapace breadth/carapace length ratio is higher in species of *Stygothelphusa* than in species of *Typhlopseudothelphusa.* However, the ratio of third pereiopod length/carapace breadth exceeds 1.6 in species of *Typhlopseudothelphusa,* whereas in species of *Stygothelphusa* this ratio is lower due to the proportionally wider carapace. In *S. lopezformenti* the eyes are still complete, although the elongation of appendages and the lack of pigmentation suggest a troglobitic life style.

Acknowledgments

We thank Dr. Brian Kensley for providing the first author with workspace at the National Museum of Natural History, and Dr. López-Forment for donating the type specimen of *Stygothelphusa lopezformenti.* The second author was supported by CONACyT grant PCCNCNA-031542.

Literature Cited

Alvarez, F. 1989. *Smalleyus tricristatus,* new genus, new species, and *Pseudothelphusa parabelliana,* new species (Brachyura: Pseudothelphusidae) from Los Tuxtlas, Veracruz, México.—Proceedings of the Biological Society of Washington 102: 45–49.

Pretzmann, G. 1968. Neue südamerikanische Süsswasserkrabben der Gattung *Pseudothelphusa.*—Entomologisches Nachrichten Blatt, Wien 15: 1–15.

Rathbun, M. J. 1898. A contribution to the knowledge of the fresh-water crabs of America. The Pseudothelphusinae.—Proceedings of the United States National Museum 21:507–537.

Rioja, E. 1952. Estudios carcinológicos. XXVIII. Descripción de un nuevo género de Potamonidos cavernícolas y ciegos de la Cueva del Tío Ticho, Comitán, Chis.—Anales del Instituto de Biología, Universidad Nacional Autónoma de México 23:217–225.

Rodríguez, G. 1982. Les crabes d'eau douce d'Amérique. Famille des Pseudothelphusidae.—Faune Tropicale 22:1–223.

———. 1987. Centers of radiation of freshwater crabs in the Neotropics. Pp. 51–67 *in* R. H. Gore & K. L. Heck, eds., Crustacean Issues 3: Biogeography of the Crustacea. A. A. Blakema, Rotterdam.

———, & H. H. Hobbs, Jr. 1989. Freshwater crabs associated with caves in southern México and Belize, with descriptions of three new species (Crustacea: Decapoda).—Proceedings of the Biological Society of Washington 102:394–400.

Smalley, A. E. 1964. A terminology for the gonopods of the American river crabs.—Systematic Zoology 13:28–31.

——— & D. L. Adkison. 1984. *Disparithelphusa pecki,* a new genus and species of freshwater crab from México (Brachyura: Pseudothelphusidae).—Journal of Crustacean Biology 4:127–133.

(FA) Department of Zoology, University of Maryland, College Park, MD 20742. (JLV) Colección de Carcinología, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-153, México D. F. 04510, México.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 295–298

A NEW PSEUDOTHELPHUSID CRAB FROM A CAVE IN SOUTHERN COSTA RICA (DECAPODA: BRACHYURA)

H. H. Hobbs III

Abstract.—A new species of troglophilic freshwater crab, *Pseudothelphusa puntarenas,* is described from Emus Cave in Provincia de Puntarenas, Costa Rica, Central America. This crab lacks any obvious external troglomorphic modifications, but is not yet known from epigean waters. The affinities of *P. puntarenas* with other pseudothelphusids are discussed.

Since the publication of the monograph on the Pseudothelphusidae by Rodríguez (1982), only three new species of *Pseudothelphusa* have been described (Alvarez 1987, 1989; Alvarez & Villalobos 1990), all from southern Mexico. During a joint Asociación Espeleólogica Costarricense—National Speleological Society Expedition to Costa Rica, a fourth species, described herein, was discovered from Emus Cave in Provinicia de Puntarenas and represents the first cavernicolous pseudothelphusid known from Costa Rica. This species brings the total number of Central American (Mexico, Guatemala, Belize, and Costa Rica) cave pseudothelphusids to 16 (see also Reddell 1981, Rodríguez & Hobbs 1989a, 1989b). Information concerning other cavernicolous pseudothelphusids can be found in Rodríguez (1985, 1991) and Rodríguez & Bosque (1990). Terminology follows that used by Rodríguez (1982). The following abbreviations are employed: USNM, United States National Museum (Smithsonian Institution), Washington, D.C.; IVIC, Centro de Ecologia, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela; CL, carapace length; CW, carapace width.

Pseudothelphusa puntarenas, new species
Fig. 1

Description.—Superior frontal border of carapace (Fig. 1A, C) generally smooth, divided medially by notch continuous with median groove. Inferior frontal border well defined, formed by small tubercles from which carapace rising steeply. Carapace surface (Fig. 1C) weakly convex with regions moderately well defined, gastric and branchial regions elevated; limits of epigastric regions rather obscure; broadly V-shaped cervical groove prominent, not reaching anterolateral margin. Anterolateral margin rather evenly rounded with 8–12 small denticles between orbit and cervical groove. Pterygostomian region densely setose (Fig. 1A). Third maxilliped (Fig. 1A, L) with exopod greater than half length of ischium; ischium/exopod ratio varying from 53.4–64.3, average 59.3. Chelipeds unequal, right chela (Fig. 1B) generally more robust than left with mildly sinuous ventral margin; fingers of major chelae gaping, curved, and weakly punctate; teeth on opposable cutting surfaces of finger of moderate size. Ventral view of body as in Fig. 1K. Eyes well developed, pigmented; carapace mottled with tan, brown, and reddish-brown pigmentation.

First male gonopod (Fig. 1D–G) with distal half arched laterally and with prominent triangular-shaped cephalic process; reniform mesial process well developed. Gonopod bearing short, stiff setae on middle part of mesial margin and few long setae on proximal half; apical cavity (Fig. 1J) elongated along caudo-cephalic axis, bearing se-

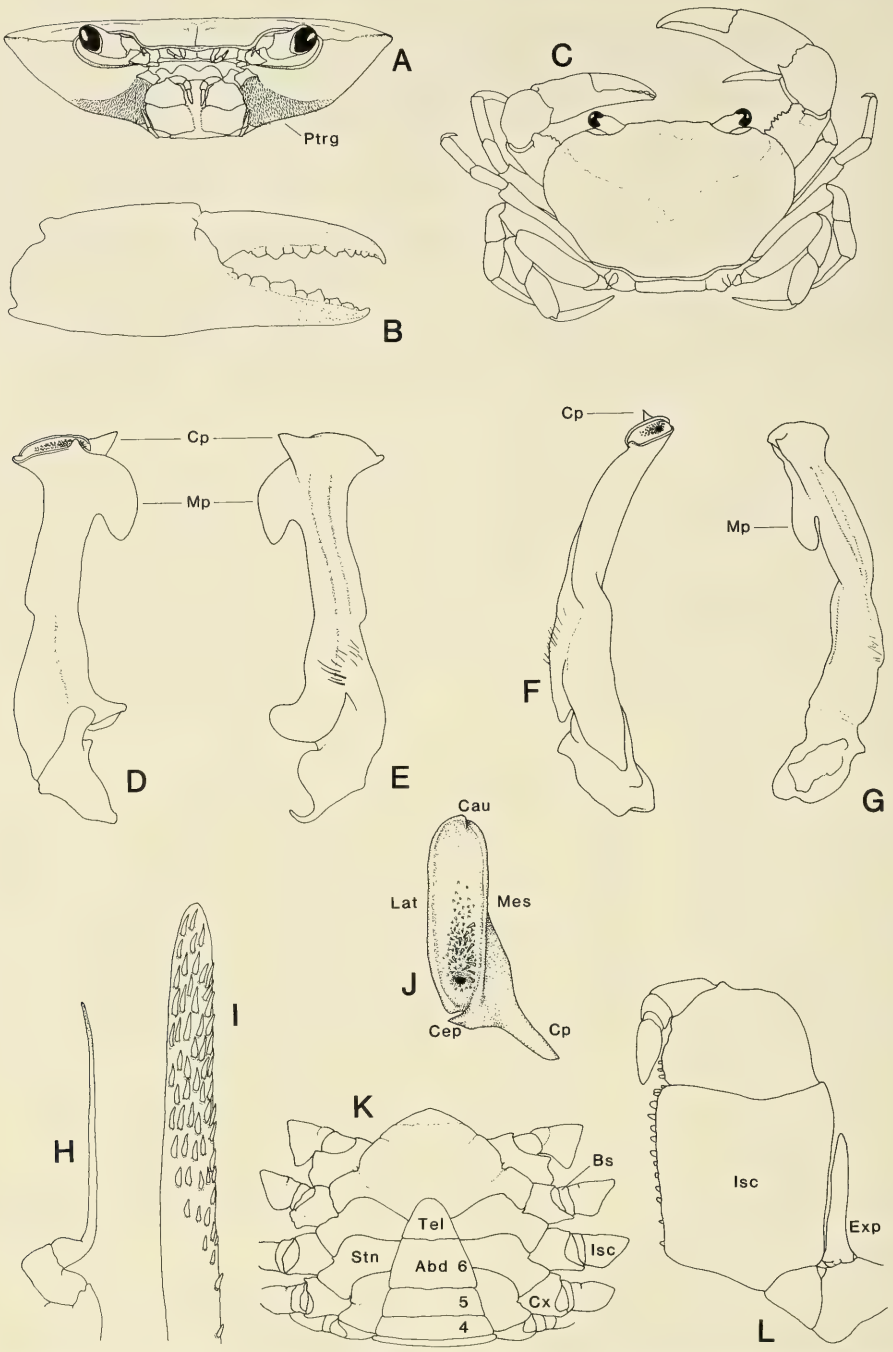


Fig. 1. *Pseudothelphusa puntarenas,* new species: A, frontal view of carapace, orbital and buccal region; B, right chela; C, dorsal view of crab; D, lateral view of left first gonopod of male; E, mesial view of same; F, caudal view of same; G, cephalic view of same; H, caudal view of male second gonopod; I, distal part of male second gonopod; J, apical view of male left first gonopod; K, sternum and abdomen, ventral view; L, left third maxilliped (setae not shown). (Abd: Abdomen; Bs: Basis; Cau: Caudal; Cep: Cephalic; Cp: Cephalic process; Cx: Coxa; Exp: Exopod; Isc: Ischium; Lat: Lateral; Mes: Mesial; Mp: Mesial process; Ptrg: Pterygostomian region with setae; Stn: Sternite; Tel: Telson).

tae over middle and cephalic end of cavity; terminal pore setae most densely distributed toward cephalomesial portion of cavity; borders of cavity of equal thickness with mesial one slightly elevated above lateral border; opening of sperm channel situated cephalically. Second male gonopod (Fig. 1H, I) extending to or slightly beyond apical end of gonopod; terminal part covered by numerous oblique rows of closely arranged spinules.

Type material.—Holotype: male, CL = 11.7 mm, CW = 18.3 mm, USNM 250555; paratypes: 3 males, CL = 9.7, 12.95, 8.3 mm, CW = 15.4, 21.5, 13.0 mm; 7 females, CL = 8.2, 10.5, 13.9, 15.9, 13.5, 11.2, 13.7 mm, CW = 12.9, 16.0, 22.6, 25.9, 22.1, 18.1, 22.1 mm, USNM; 1 male, IVIC.

Type locality.—Small stream in Emus Cave, Provincia de Puntarenas, Costa Rica. The crabs were found approximately 120 m from the entrance in pools and small riffle areas with rubble-cobble-gravel limestone substrates. The stream in Emus Cave on 1 January 1989 (temperature 24.3°C) resurged about 23 m in elevation below the entrance and flowed directly into the Rio Claro. A species of *Macrobrachium* (probably *M. carcinus* (Linnaeus)) was observed but not collected, as were individuals of an unidentified catfish.

Etymology.—This species is named for the Province, Puntarenas, where the cave is located in southwestern Costa Rica.

Relationships.—Although few external morphological characteristics have been demonstrated to have taxonomic value within the pseudothelphusids (Rodríguez 1982), the gonopod, however, has proven to be an important structure for distinguishing species. The distal part of the gonopod of the male of *P. puntarenas* shows similarities to that of *P. leiophrys* Rodríguez & Smalley, 1969, *P. galloi* Alvarez & Villalobos, 1990, *P. granatensis* Rodríguez & Smalley, 1969, *P. jouyi* Rathbun, 1893, *P. parabelliana* Alvarez, 1989, and *P. mexicana* Alvarez, 1987. The gonopods of all these species have a well developed mesial process but in *P. puntarenas, P. galloi,* and *P. leiophrys* the outer margin is smooth, whereas it is serrate in the other species. The apex of the gonopod of *P. mexicana, P. parabelliana,* and *P. granatensis* has a well developed lateral lobe with three, two, and two projections, respectively, while *P. puntarenas* lacks a well developed lateral lobe. In general, the gonopod morphology of *P. puntarenas* is closer to that of *P. leiophrys,* but can easily be separated from it by the well developed cephalic process in *P. puntarenas.*

Acknowledgments

Appreciation is extended to the members of the 1989 Asociación Espeleológica Costarricense—National Speleological Society Expedition for their assistance in the field. Special thanks are extended to D. Dotson, Expedition Leader, who invited me to go to Costa Rica and to F. Grady who helped collect the crab specimens. I am also grateful to H. H. Hobbs, Jr., and G. Rodríguez for their criticisms of the manuscript. This work was supported in part by grants received from The Faculty Research Fund Board and the Faculty Development Organization of Wittenberg University.

Literature Cited

Alvarez, F. 1987. *Pseudothelphusa mexicana,* a new freshwater crab from the State of Guerrero, Mexico (Brachyura: Pseudothelphusidae).—Proceedings of the Biological Society of Washington 100:1–3.

———. 1989. *Smalleyus tricristatum,* new genus, new species, and *Pseudothelphusa parabelliana,* new species (Brachyura: Pseudothelphusidae) from Los Tuxtlas, Veracruz, Mexico.—Proceedings of the Biological Society of Washington 102:45–49.

———, & J. Villalobos. 1990. *Pseudothelphusa galloi,* a new species of freshwater crab (Crustacea: Brachyura: Pseudothelphusidae) from southwestern Mexico.—Proceedings of the Biological Society of Washington 103:103–105.

Rathbun, M. 1893. Descriptions of new species of American fresh-water crabs.—Proceedings of the

United States National Museum 16(959):649–661.

Reddell, J. R. 1981. A review of the cavernicole fauna of Mexico, Guatemala, and Belize.—Bulletin of the Texas Memorial Museum 27:1–327.

Rodríguez, G. 1982. Les crabes d'eau douce d'Amérique. Famille des Pseudothelphusidae.—Office de la Recherche Scientifique et Technique Outre-Mer, Faune Tropicale 22:1–223.

———. 1985. A new cavernicolous crab (Crustacea, Decapoda, Pseudothelphusidae) from Columbia.—Biologia Vest 33(2):73–80.

———. 1991. The freshwater crabs of America: Family Trichodactylidae, and supplement to the family Pseudothelphusidae.— Faune Tropicale ORSTOM (in press).

———, & C. Bosque. 1990. A stygobiont crab, *Chaceus caecus* n. sp., and its related stygophile, *Chaceus motiloni* Rodriguez, 1980, (Crustacea, Decapoda, Pseudothelphusidae) from a cave in the Cordillera de Perija, Venezuela.—Mémoires de Biospeologie 17:127–134.

———, & H. H. Hobbs, Jr. 1989a. A new cavernicolous crab, *Zilchia falcata,* from Guatemala, with notes on the genera of the Potamocarcinini (Crustacea, Decapoda, Pseudothelphusidae).—Bulletin du Museum National d'Histoire Naturelle, 4th Serie 11(1):183–192.

———. 1989b. Freshwater crabs associated with caves in southern Mexico and Belize, with descriptions of three new species (Crustacea: Decapoda).—Proceedings of the Biological Society of Washington 102:394–400.

———, & A. E. Smalley. 1969. Los Cangrejos de agua dulce de México de la familia Pseudothelphusidae (Crustacea, Brachyura).—Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Ciencias Mar y Limnología 40:69–112.

Department of Biology, Wittenberg University, P.O. Box 720, Springfield, Ohio 45501-0720.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 299–308

CHIROSTYLID AND GALATHEID CRUSTACEAN ASSOCIATES OF COELENTERATES AND ECHINODERMS COLLECTED FROM THE *JOHNSON-SEA-LINK* SUBMERSIBLE, INCLUDING A NEW SPECIES OF *GASTROPTYCHUS*

A. L. Rice and J. E. Miller

Abstract.—A new species of chirostylid decapod crustacean, *Gastroptychus salvadori,* is described from a specimen collected in association with a brisingid starfish by submersible off the Bahamas. A number of other chirostylids and galatheids, collected together with their echinoderm associates in the tropical and sub-tropical western Atlantic, are also reported. Some of these associations were previously unsuspected. The collections suggest that at least some of the decapods live together as mated pairs on their hosts.

Traditional benthic sampling gears such as trawls and dredges disrupt any but the most robust associations between different animal species. Nevertheless, there are numerous reports in the literature of behavioural associations between decapod crustaceans and other benthic organisms, particularly coelenterates, sponges and echinoderms. Moreover, evidence for such associations has been found even in the fossil record (Bishop & Portell 1989). Most of these records are from relatively shallow regions, but the use of manned submersibles permits observations of such associations to be extended to deeper waters, and particularly to areas where the use of more conventional sampling techniques is precluded. Observations, photographs and collections made from the *Johnson-Sea-Link* (JSL) submersibles (Harbor Branch Oceanographic Institution, Inc.) in the tropical and sub-tropical western Atlantic during recent years have already provided data on associations between pontoniine shrimps and deep sea echinoids (Bruce 1986a, 1986b; Berggren & Svane 1989). This paper reports a small collection of galatheoid crustaceans secured along with their associates during these and other dives off the Caribbean islands of Barbados and St. Vincent. Material described herein has been deposited at the National Museum of Natural History, Smithsonian Institution (USNM) and the Harbor Branch Oceanographic Museum (HBOM).

Family Chirostylidae

Gastroptychus salvadori, new species

Figs. 1A–D; 2B, D, F

Material.—1 ovig. female (holotype USNM 239278)JSL-I-2264, off San Salvador Island, Bahamas, 24°03.61′N, 74°33.37′W, 13 Sep 1988, 874 m, associated with the brisingid starfish *Novodinia antillensis* (A. H. Clark).

Description. (Figs. 1, 2)—Carapace length excluding rostrum slightly more than greatest breadth. Branchial regions inflated so that carapace narrows both anteriorly and posteriorly. Rostrum slender, upturned, more than ⅓ length of remainder of carapace.

Linea anomurica distinct, almost straight; beneath it carapace flanks more or less evenly covered with small spines except for a small, naked, depressed area immediately above insertion of cheliped.

Above linea anomurica carapace surface covered with close-set spines, of which about 45 significantly enlarged; spination particularly dense in cardiac and branchial regions.

Regions of carapace rather clearly demarcated by grooves, carrying the following complement of enlarged spines; gastric region with 3 unpaired and about 6 paired spines; small, triangular anterolateral regions each with 1 spine; hepatic regions with 1 spine; epibranchial regions with 2 large spines; metagastric region with 1 pair of large spines and about 5 intermediate spines; branchial regions each with row of 4 or 5 moderately enlarged spines and additional large spine near mid-line; small, median, posterior, triangular "cardiac" region with pair of enlarged spines. Row of curved, dorsally directed spines along posterior carapace border which also carries about 10 small spines directed posteriorly and clearly visible in dorsal view.

Abdominal tergites covered with close-set setae, much more abundant than on carapace. First abdominal tergite narrow; posterior margin a raised, rounded ridge carrying about 30 short spines and ending in two stout, spine-like processes representing reduced pleura. Pleura of somites 2–5 well-developed, those of somite 2 being acutely tipped, with concave anterior margin, remainder becoming successively more rounded posteriorly. Second tergite with raised transverse ridge anteriorly, interrupted in mid-line and carrying spines similar to those on first tergite; this spination continued onto pleura, but becoming sparse towards tip. Third, fourth and fifth tergites with no significant spines, pleura all carrying low, blunt spines becoming more prominent posteriorly. Sixth tergite and pleura with numerous short spines, generally becoming more prominent posteriorly and about 9 projecting from posterior margin of tergite. Telson membranous, carrying setae but no spines, consisting of 2 small proximal and 2 larger distal rounded lobes so that posterior telson margin has shallow median indentation. Telson and uropods folded tightly beneath sixth abdominal somite.

Sternum narrowed anteriorly. Small plates at base of third maxillipeds each carry a single spine; kite-shaped plates between chelipeds each bear 2 prominent acute spines anteriorly and about 9 smaller ones; sternal plates between second pair of legs with blunt tubercles, those between third and fourth legs unarmed. Sternite of fifth legs atrophied.

When extended, antennular peduncle over-reaches rostrum by length of third segment; basal segment with blunt outer lobe armed with setae but no spines.

Antennal peduncle short, extending just beyond eye; basal segment with short outer spine; terminal peduncular segment with slender distoventral spine.

Coxa of third maxilliped with strong, curved spine on lower external angle; basis with short spine on inner distal margin; ischium with row of 11–12 subequal teeth on inner margin; merus with very short, slightly hooked spine on outer distal margin; carpus with blunt projection basally on outer margin; propodus and dactyl without spines.

Chelipeds and ambulatory legs long, slender, very spinous; propodus, carpus, merus and ischium each with 6 longitudinal rows of principal spines and several subsidiary rows of smaller spines.

Chelipeds about 6 times as long as carapace and rostrum. Basis with single strong ventrodistal spine. Dactyl more than $\frac{1}{3}$ length of propodus, biting edge carrying large proximal truncated spine with denticulate summit closing between two similar spines on propodus; otherwise biting edges of both propodus and dactyl armed with series of small spines which are particularly close-set distally, beyond gape.

Legs 2–4 subequal, reaching about $\frac{4}{5}$ length of carpus of chelipeds. Ratio of dactyl length to propodus length decreasing from ca. 0.3 in leg 2 to ca. 0.2 in leg 4; ratio of propodus length to carpus length increasing from ca. 1.2 in leg 2 to ca. 1.33 in leg 4. Dac-

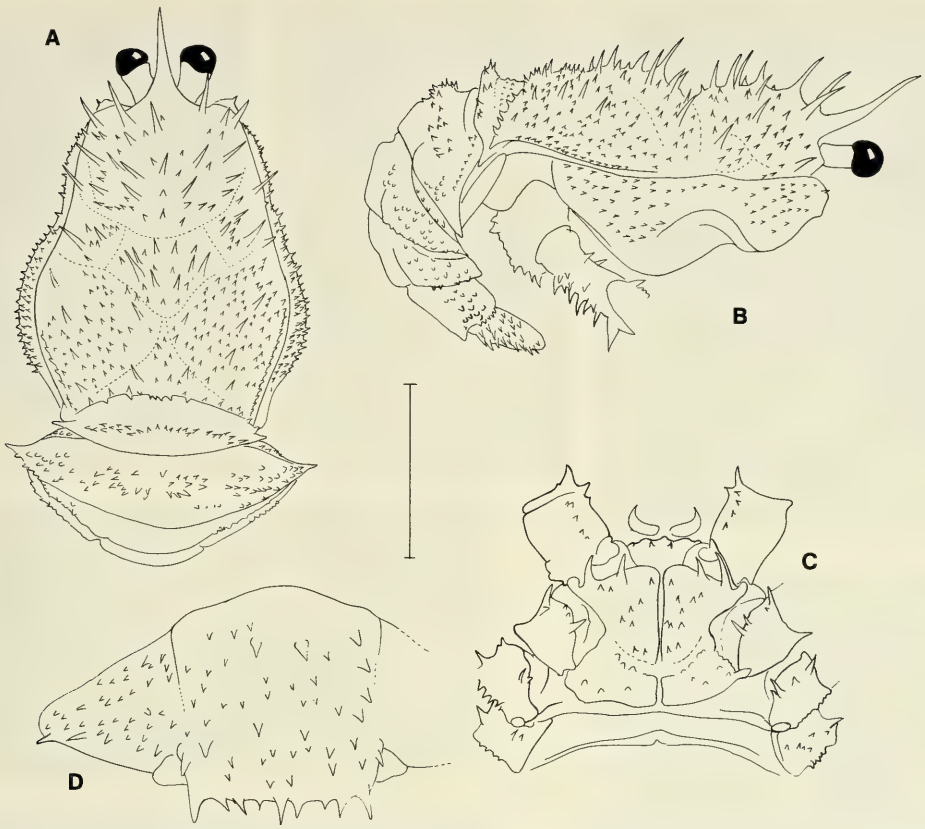


Fig. 1. *Gastroptychus salvadori,* new species. Holotype: A, dorsal view of carapace and first two abdominal tergites; B, lateral view; C, sternal plates; D, dorsal view of sixth abdominal somite. Scale equals 10 mm (A, B), and 5 mm (C, D).

tyls each with single row of 8 or 9 ventral spines regularly increasing in length distally. Propodus of each leg with 6 longitudinal spine rows of which only the ventral extends along whole length of segment: ventral rows with 20–23 spines, including distal pair between which dactyl bites; dorsal rows with 20–23 spines; ventro-lateral and ventro-mesial rows with 9–14 spines; dorso-lateral and dorso-mesial rows with 18–21 spines. Coxo-basal joints each with prominent distal and proximal ventral spines and several smaller spines.

Fifth legs greatly reduced, without spines; dactyl, propodus and carpus with long setae. Chelate, with dactyl about $\frac{1}{5}$ length of propodus.

Abdomen of holotype female carrying about 50 eggs, 1.5–2.2 mm in diameter.

Measurements of holotype.—Carapace length 22.6 mm (including rostrum), 17.5 mm (excluding rostrum), maximum carapace width 15.9 mm, total length of chelipeds ca. 135 m, left dactyl length 17.7 mm, left propodus length 45.6 mm.

Color.—In life the holotype was generally orange-red, with starkly contrasting white patches, particularly on the carapace and abdomen. The orange coloration on the legs was most intense on and at the bases of the main spine rows, with rather paler areas between the rows, giving the general impression of longitudinal stripes along the limbs. On the carapace the color was most intense

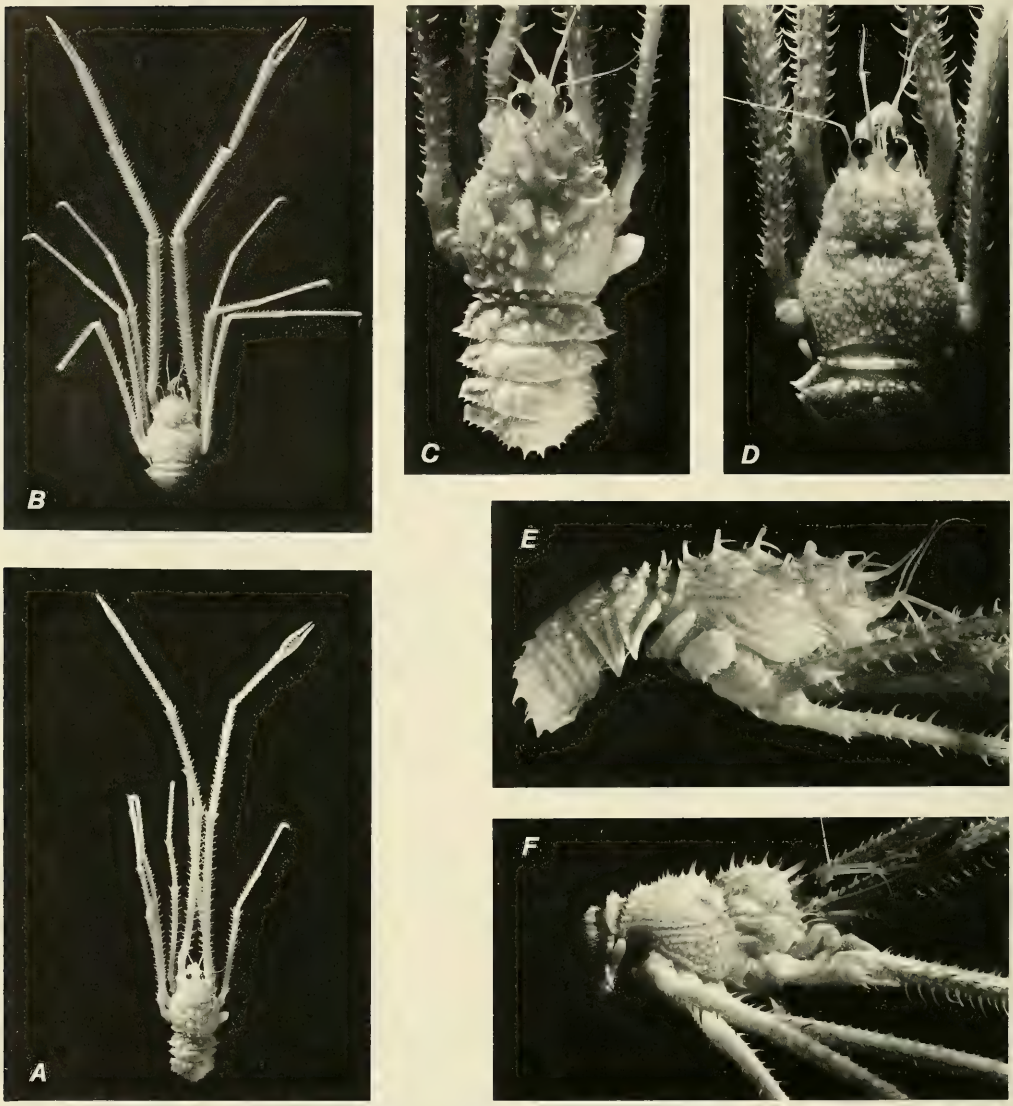


Fig. 2. Comparison of a specimen of *Gastroptychus formosus* (Filhol, 1885) (A, C, E) with the holotype of *G. salvadori* new species (B, D, F). A, B dorsal view; C, D dorsal view; E, F lateral view. A, C, E: female (carapace length including rostrum, 20 mm) collected off north-west Spain, 42°15′N, 11°22′W, Discovery Stn. 9042, 1541–1662 m, Discovery Collections, Institute of Oceanographic Sciences Deacon Laboratory, Wormley, U.K.

on the anterior half of the rostrum, on the gastric and hepatic regions and on the cardiac region. The coloration was much less intense on the branchial regions, while pure white areas were present at the base of the rostrum, across the frontal region, on the antero-lateral regions, across the region of the cervical groove and the epibranchial regions, and along the posterior carapace margin. The anterior part of each abdominal tergite was also white.

Remarks.—The chirostylid species traditionally placed in the genus *Chirostylus* Ortmann, 1892 (e.g., Van Dam 1933, Chace 1942) were separated into two genera by Miyake & Baba (1968); three species lacking

Table 1.—Comparison of *Gastroptychus salvadori,* new species, with Atlantic congeners.

	G. spinifer	*G. affinis*	*G. formosus*	*G. salvadori*
Carapace				
Max. length	30+ mm	11 mm	25+ mm	23 mm
Spination	dense	sparse	sparse	dense
Enlarged spines	ca. 20	<20	ca. 25	>40
Chelipeds				
Total length	4.4–7.1 × CL	3.5–5.6 × CL	5–6 × CL	ca. 6 × CL
Merus L/W ratio	?	?	ca. 21	ca. 14
Dactyl/propodus length	?	?	ca. 0.3	ca. 0.4
Abdominal tergites				
1	unarmed	unarmed	ca. 10 spines	>20 spines
2	unarmed	unarmed	ca. 15 spines	>25 spines
3	unarmed	unarmed	ca. 10 spines	ca. 10 spines
4	unarmed	unarmed	ca. 10 spines	ca. 50 spines
Sternal plates	1–2 large spines	1 large spine	2–3 large spines	2 large + ca. 10 small spines
3rd maxillipeds				
Merus outer spine	prominent	prominent	prominent	very small
Carpus outer spine	prominent	prominent	prominent	absent

a distinct rostrum were retained in the genus *Chirostylus,* while those species with a distinct spiniform rostrum were transferred to the genus *Gastroptychus* Caullery, 1896. The latter genus, as it is now constituted (Baba 1988, Baba & Haig 1990), contains 17 species, three of which are reported from the Atlantic: *G. spinifer* (Milne Edwards, 1880) and *G. affinis* (Chace, 1942) being restricted to the West Indian region (Chace 1942, Springer & Bullis 1956), while *G. formosus* (Filhol, 1885) is reported from the Eastern Atlantic in the Bay of Biscay and off the coast of Ireland and the Canaries (Selbie 1914). These species can be distinguished from one another, and from *G. salvadori,* by a combination of overall size, spination of the carapace, abdominal tergites, sternum and third maxillipeds, and the relative length and robustness of the chelipeds (Table 1).

Of the three previously described *Gastroptychus* species, *G. salvadori* is most similar to *G. formosus,* both species having some of the abdominal tergites armed with spines, whereas these tergites are totally unarmed in *G. affinis* and *G. spinifer.* Moreover, while *G. affinis* and *G. spinifer* both have a row of enlarged spines along the mid-dorsal line of the carapace, such a median row is not a feature of either *G. formosus* or *G. salvadori.*

G. salvadori differs from *G. formosus* in having rather more robust chelipeds and in being generally much more spinous (Fig. 2). Thus, the dorsal and lateral surfaces of the carapace in *G. salvadori* are everywhere covered with rather close-set spines of which about 40 are significantly enlarged; in *G. formosus* only about 25 of the carapace spines are significantly enlarged, while the smaller subsidiary spines are sparse on the branchial region and virtually absent from the gastric, hepatic and epibranchial regions. Similarly, while the first and second abdominal tergites in both *G. salvadori* and *G. formosus* each carry a transverse irregular series of spines, these are much smaller and more numerous in *G. salvadori.* The pleural plates of the third to sixth abdominal somites are armed with a series of spines, becoming more pronounced posteriorly in both species; again, these are much smaller, but

more abundant in *G. salvadori* than in *G. formosus.* The only exception is the tergite of the fifth abdominal somite which carries 4 pairs of prominent spines close to the mid-line in *G. formosus* [not unarmed as Selbie (1914:63) suggests], whereas this tergite is furnished only with setae in *G. salvadori.* The tergite of the sixth abdominal somite carries about 12 large spines in *G. formosus,* including three on the posterior margin, while this tergite in the holotype of *G. salvadori* carries about 50 small spines, of which nine are ranged along the posterior margin.

The sternal plates between the chelipeds are also quite different in the two species. In both cases the anterior border, close to the insertion of the cheliped, carries two very prominent spines on each side. However, whereas in *G. formosus* there is an additional large spine posteriorly near the mid-line, this spine is replaced by a series of about 10 smaller spines in *G. salvadori.*

Finally, the meral and carpal joints of the third maxillipeds each carry a prominent spine distally on the outer margin in *G. formosus,* as in *G. spinifer* and *G. affinis,* but in *G. salvadori* the carpus is unarmed, while the merus has only an extremely small hooked spine in this position.

Etymology.—Named for the type locality, San Salvador Island, Bahama Islands.

Habitat notes.—When first sighted from the submersible, the chirostylid was sheltering on the sediment surface at the base of a large mass of the oculinid coral, *Madrepora carolina* (Pourtalès). On the surface of the coral there were a number of large (ca. 70 cm diameter) specimens of the brisingid seastar *Novodina antillensis,* several of which were collected. As one of the brisingids was being lifted from the coral with the submersible's manipulator arm, the chirostylid 'leapt' onto the starfish and was collected along with it.

The general orange-red color of the chirostylid, traces of which remain on the spine tips in the preserved specimen, closely matched that of the brisingid but contrasted starkly with the very pale, almost white, coloration of the coral. This color match, along with the spinous morphology and the curious behaviour of the chirostylid, suggests that *G. salvadori,* and perhaps other *Gastroptychus* species, may live in close association with brisingids or similar organisms. The abundant spination of the body, and particularly the limbs, in the genera *Chirostylus* and *Gastroptychus,* on the other hand, would seem to be disadvantageous if they lived on finely branching organisms such as gorgonians. Such organisms are known to be frequented by relatively smooth-bodied chirostylids such as *Uroptychus* (e.g., Pequegnat & Pequegnat 1970: 161). However, an uncollected chirostylid which appears to belong to *G. salvadori* was photographed from the *Johnson-Sea-Link* on a species of the arborescent gorgonian genus *Keratoisis* (family Isididae) some 40 nautical miles east of Fort Pierce, Florida at a depth of 731 m. Clearly, *Gastroptychus* species also crawl over such branching organisms, through the color match in this case between the galatheid and the gorgonian was much less close than that between the holotype and the brisingid.

Uroptychus capillatus Benedict, 1902

Material.—1 male, 1 ovig. female (USNM 252390), 1 male, 1 ovig. female (HBOM 089:6819), JSL-I-2260, off Conception Island, Bahamas, 23°48.8′N, 75°08.1′W, 11 Sep 1988, 573 m; associated with the comatulid crinoid *Crinometra brevipinna* (Pourtalès) (see Discussion).

Remarks.—*U. capillatus* has been reported previously only twice in the literature, originally by Benedict (1902) from an *Albatross* station near Arrowsmith Bank off the east coast of Yucatan, and subsequently by Chace (1942) from an *Atlantis* station off the north coast of Cuba. Although Benedict mentioned two specimens in his rather inadequate original account, one of these seems to have disappeared by the 1940s

since Chace refers only to "Benedict's type" (a female in rather poor condition) in addition to his own single specimen, an ovigerous female, pointing out that both individuals lack chelipeds. The specimens reported here agree closely with Benedict's type (USNM 20565) and, together with the type, will be used as the basis for a redescription of the species, including the male (Rice, in prep.).

The morphologically similar congener, *Uroptychus rugosus* (A. Milne Edwards, 1880), also from the Caribbean region, is reported to live commensally with a crinoid, probably *Stylometra spinifera* (Chace, 1942).

Family Galatheidae
Munidopsis abdominalis
(A. Milne Edwards, 1880)
Fig. 3A, B, C

Material.—1 male, 1 ovig. female (USNM 239277), JSL-I-2269, off Crooked Island, Bahamas, 22°41.5′N, 74°20.8′W, 16 Sep 1988, 569 m, on a specimen of the echinoid *Cidaris blakei* (A. Agassiz) (see Fig. 3A). 1 male (USNM 239273), JSL-I-2269, as above, 543 m, on *Cidaris blakei* (Fig. 3B). 1 male (USNM 239276), JSL-II-1733, off Bridgetown, Barbados, 13°00.70′N, 59°39.53′W, 18 Apr 1989, 417 m, on *Cidaris blakei.* 1 male, 1 ovig. female (HBOM 089:06820), JSL-II-1743, off York Bay, St. Vincent, 13°07.2′N, 61°17.04′W, 23 Apr 1989, 408 m, on *Cidaris rugosa* (H. L. Clark) (Fig. 3C).

Remarks.—Both *M. abdominalis* and *C. blakei* were originally described from material collected during the three cruises of the *Blake* in 1877–1880, the decapods having been taken at a station off Barbados (Milne Edwards 1880) and the echinoid at several localities off the coast of Cuba (Agassiz 1878). *Cidaris blakei* has been taken subsequently at a number of localities in the Florida-West Indian region at depths from 150 and 790 m (Serafy 1979), while *M. abdominalis* has been reported from off Cuba, St. Kitts and from the Straits of Florida at depths from 366 to 622 m (Chace 1942, Mayo 1974). Moreover, Mayo reported that one of the stations at which *M. abdominalis* was collected was "characterized by sea urchins," though she did not identify the species. Thus, although a behavioral association between *M. abdominalis* and *C. blakei* has not been referred to previously, it may be common, if not usual.

Munidopsis alaminos
Pequegnat & Pequegnat, 1970
Fig. 3D

Material.—1 male, 1 ovig. female (HBOM 089:06821), JSL-II-1735, off Speightstown, Barbados, 13°14.9′N, 59°45.2′W, 19 Apr 1989, 722 m, associated with the holothurian *Mesothuria gargantua* Diechmann (Fig. 3D).

Remarks.—*Munidopsis alaminos* is recorded at depths ranging from about 500 m to more than 800 m in the western Atlantic and Caribbean region, from the coast of French Guiana to the northern Gulf of Mexico (Pequegnat & Pequegnat 1970, 1971; Mayo 1974). It has not been previously reported in association with any other organism.

Munidopsis spinifer
(A. Milne Edwards, 1880)
Fig. 3E, F

Material.—1 ovig. female (USNM 239275), JSL-I-2261, off Conception Island, 23°50.8′N, 75°09.6′W, 12 Sep 1988, 741 m, on the crinoid *Crinometra brevipinna* (Fig. 3E). 1 male (HBOM 089:06822); JSL-I-2269, off Crooked Island, 22°41.5′N, 74°20.8′W, 16 Sep 1988, 594 m, on *Crinometra brevipinna* (Fig. 3F). 1 juv. female (USNM 239274), JSL-II-1747, off York Bay, St. Vincent, 13°07.2′N, 61°16.8′W, 25 Apr 1989, 415 m, on *Crinometra brevipinna.*

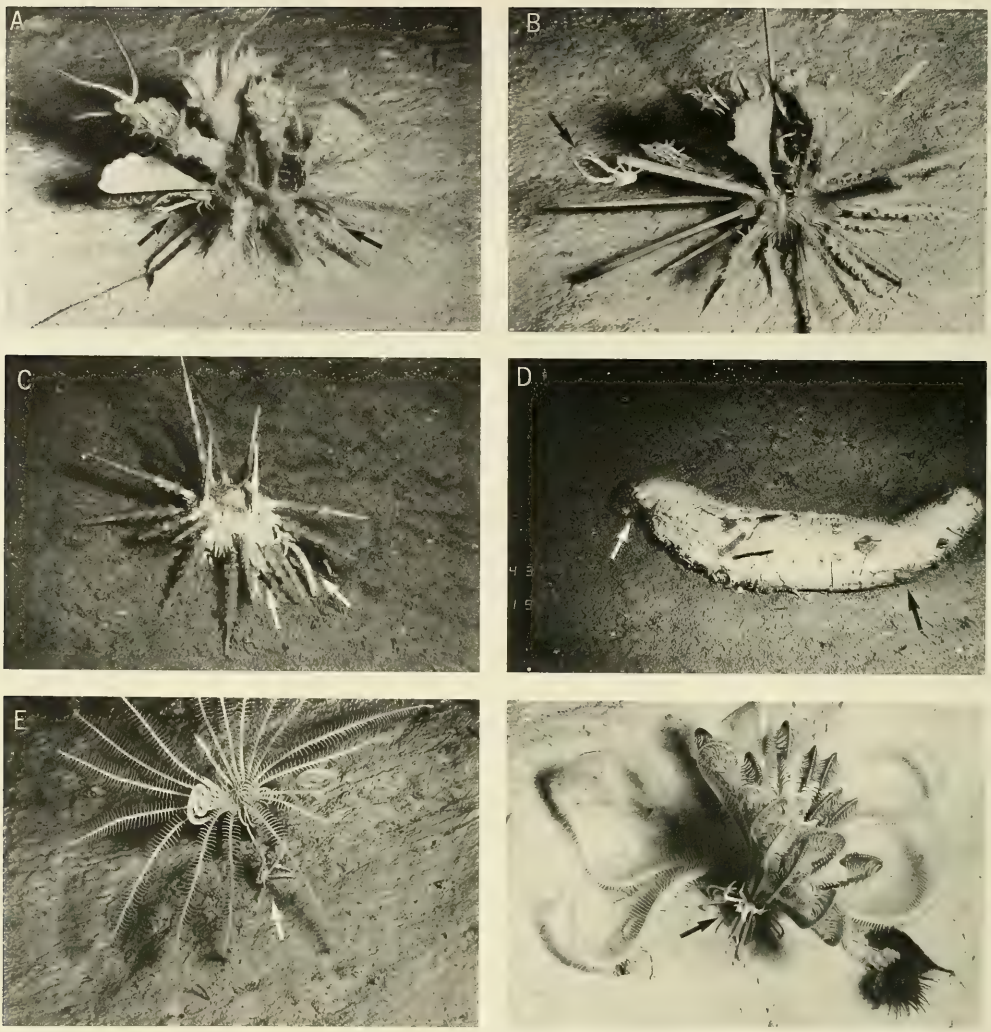


Fig. 3. Photographs of decapods (arrowed) and their echinoderm hosts, taken from the *Johnson-Sea-Link* submersible: A, *Munidopsis abdominalis* wth *Cidaris blakei,* JSL-I-2269, 569 m; B, same as A, 543 m; C, *Munidopsis abdominalis* on *Cidaris rugosa,* JSL-II-1743, 408 m; D, *Munidopsis alaminos* on *Mesothuria gargantua,* JSL-II-1735; E, *Munidopsis spinifer* on *Crinometra brevipinna,* JSL-II-2261, 741 m; F, *Munidopsis spinifer* on *Crinometra brevipinna,* JSL-I-2269, 594 m.

Remarks.—Munidopsia spinifer is recorded in the western Atlantic from the Bahamas and the Straits of Florida, and off the Greater and Lesser Antilles from Cuba to Barbados in depths ranging from 275 m to 880 m (Milne Edwards & Bouvier 1897, Chace 1942, Mayo 1974).

Mayo reports the species as being strikingly pigmented orange-red contrasting with white. The contrast appears as longitudinal banding on the chelipeds and ambulatory legs, as in *Chirostylus salvadori,* but whereas the banding on the carapace and abdomen in *C. salvadori* is transverse, it is longitudinal in *M. spinifer.* Thus, the rostrum and frontal region of *M. spinifer* are orange-red, with this pattern extended posteriorly as broad bands on either side of the mid-line.

These bands are continued onto the abdominal somites, with white bands medially and on the lateral margins.

Discussion

There are numerous records in the literature of behavioral associations between galatheoid decapods and other organisms, particularly coelenterates and echinoderms (Milne Edwards 1880; Chace 1942; Baba 1974, 1979, 1988; Pequegnat & Pequegnat 1970). Where the species concerned are littoral or shallow-living, these records are frequently based on direct observations and are therefore unequivocal [e.g., records of *Allogalathea elegans* (Adams & White, 1848), associated with crinoid genera, as cited by Baba (1979, 1988)]. For deeper-living forms, the records are based largely on trawl and dredge hauls and are often less convincing. Thus, although there is rather strong evidence for an association between *Uroptychus nitidus* (A. Milne Edwards, 1880) and the gorgonian coral genus *Chrysogorgia* (see Pequegnat & Pequegnat 1970) and between *Gastroptychus novaezelandiae* Baba, 1974 and the pennatulid *Balticina willemoesii* (see Baba 1974), the evidence for a similar association between *Uroptychus rugosus* (A. Milne Edwards, 1880) and crinoid species, as reported by Chace (1942), is largely circumstantial. Nevertheless, the direct observations reported here, along with the indirect evidence, suggest that some form of commensalism is characteristic of many if not most species of galatheid and chirostylid decapods. This may even be true of the smaller species of genera such as *Munidopsis,* in which commensalism has never been reported before, though this life-style is, perhaps, not to be expected of the deeper-living and larger representatives of the genus.

Moreover, three of the five decapod species reported here were collected in pairs, in each case consisting of a male and an ovigerous female, apparently monopolizing a single host specimen. This raises the intriguing possibility that the animals may form permanent or semi-permanent breeding relationships, a situation never described before in this group.

Acknowledgments

Funding for submersible dives was granted through Harbor Branch Oceanographic Institution, Inc. (HBOI) and the Smithsonian Institution (SI). We are grateful to the crews of the *Johnson-Sea-Link* submersibles and the research vessels *Seward Johnson* and *Edwin Link,* all at HBOI, for their assistance during several missions to the Bahama Islands and the Lesser Antilles. Our thanks are due to Dr. Frederick M. Bayer (SI) for identifying the gorgonian, *Keratoisis,* photographed with the suspected, but uncollected, second specimen of *Gastroptychus salvadori*; the photo was kindly supplied by HBOI submersible pilot, Mr. D. Liberatore. Dr. C. Young (HBOI) provided us with specimens and photographs of *Munidopsis alaminos* and *Mesothuria gargantua* from one of his submersible dives off Barbados. This paper is HOBI Contribution No. 807 and Contribution No. 17—Studies on bathyal echinoderms of the Bahama Islands, J. E. Miller (HBOI), Principal investigator.

Literature Cited

Adams, A., & A. White. 1848. Crustacea. I–VIII + 60 pp. *in* A. Adams, ed., The zoology of the voyage of H.M.S. *Samarang*; under the command of Capt. Sir E. Belcher . . . during . . . 1843–46. London.

Agassiz, A. 1878. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, by the U.S. Coast Steamer *Blake.* II. Report on the Echini.—Bulletin of the Museum of Comparative Zoology, Harvard College 5(9):181–195.

Baba, K. 1974. Four new species of galatheidean Crustacea from New Zealand waters.—Journal of the Royal Society of New Zealand 4:381–393.

———. 1979. Expéditions Rumphius II (1975). Crustacés parasites, commensaux, etc. (Th. Monod et R. Serène, éd.) VII. Galatheid crustaceans (Decapoda, Anomura).—Bulletin du Muséum

National d'Histoire Naturelle Paris, 4e sér, 1, section A, no. 3:637–657.

———. 1988. Chirostylid and galatheid crustaceans (Decapoda: Anomura) of the "Albatross" Philippine Expedition, 1907–1910.—Researches on Crustacea Special No. 2:203 pp.

———, & J. Haig. 1990. A new species of chirostylid crustacean (Decapoda: Anomura) from off the west coast of North America.—Proceedings of the Biological Society of Washington 103:854–860.

Benedict, J. E. 1902. Descriptions of a new genus and forty-six new species of crustaceans of the family Galatheidae, with a list of the known marine species.—Proceedings of the United States National Museum 26:243–334.

Berggren, M., & I. Svane. 1989. *Periclimenes ingressicolumbi,* new species, a pontoniine shrimp associated with deep-water echinoids off San Salvador Island in the Bahamas, and a comparison with *Periclimenes milleri.*—Journal of Crustacean Biology 9:432–444.

Bishop, G. A., & R. W. Portell. 1989. Pliocene crab–sea star association from southwest Florida.—Journal of Crustacean Biology 9:453–458.

Bruce, A. J. 1986a. *Diapontonia maranulus,* new genus, new species, a pontoniine shrimp associate of a deep-water echinoid.—Journal of Crustacean Biology 6:125–133.

———. 1986b. *Periclimenes milleri* new species, a bathyal echinoid-associated pontoniine shrimp from the Bahamas.—Bulletin of Marine Science 39:637–645.

Caullery, M. 1896. Crustacées Schizopodes et Décapodes. Pp. 365–419 *in* R. Koehler, ed., Résultats scientifiques de la campagne du "Caudan" dans le Golfe de Gascogne—Aout–Septembre 1895.—Annales de l'Université de Lyon 26:740 pp.

Chace, F. A. 1942. The anomuran Crustacea. I. Galatheidea. Reports of the Scientific Results of the Atlantis expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University.—Torreia 11:1–106.

Filhol, H. 1885. La Vie au Fond des Mers. Les explorations sous-marines et les voyages du Travailleur et du Talisman. Paris, 301 pp.

Mayo, B. S. 1974. The systematics and distribution of the deep-sea genus *Munidopsis* (Crustacea, Galatheidae) in the western Atlantic Ocean. Unpublished Ph.D. dissertation, University of Miami (UM 75/04156), 432 pp.

Miyake, S., & K. Baba. 1968. On the generic characters of *Chirostylus,* with description of two Japanese species (Crustacea, Anomura).—Journal of the Faculty of Agriculture, Kyushu University, Fukuoka 14:379–387.

Milne Edwards, A. 1880. Reports on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea. 8. Études préliminaires sur les Crustacés.—Bulletin of the Museum of Comparative Zoology, Harvard College 8(1):1–68.

———, & E. L. Bouvier. 1897. Reports on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), in the Caribbean Sea (1878–79) and along the Atlantic coast of the United States (1880), etc. XXXV. Description des Crustacés de la famille des Galathéidés recueillis pendant l'Expedition.—Memoirs of the Museum of Comparative Zoology at Harvard College 19:1–141.

Ortmann, A. 1892. Die Decapoden-Krebse des Strassburger Museums.—Zoologische Jahrbücher, Jena 6:241–326.

Pequegnat, L. H., & W. E. Pequegnat. 1970. Deep-sea anomurans of superfamily Galatheoidea with descriptions of three new species. Pp. 125–170 *in* W. E. Pequegnat & F. A. Chace, eds., Contributions on the biology of the Gulf of Mexico, Vol. 1. Gulf Publishing Co., Houston, Texas.

Pequegnat, W. E., & L. H. Pequegnat. 1971. New species and new records of *Munidopsis* (Decapoda: Galatheidae) from the Gulf of Mexico and Caribbean Sea.—Texas A&M University Oceanographic Studies 1(supplement):1–24.

Selbie, C. M. 1914. The Decapoda Reptantia of the coasts of Ireland. Part I. Palinura, Astacura and Anomura (except Paguridea).—Fisheries Ireland, Scientific Investigations 1:1–116.

Serafy, D. K. 1979. Echinoids (Echinodermata: Echinoidea).—Memoirs of the Hourglass Cruises. Florida Department of Natural Resources Marine Research Laboratory V (III):120 pp.

Springer, S., & H. R. Bullis. 1956. Collections by the *Oregon* in the Gulf of Mexico. List of crustaceans, mollusks, and fishes. Identified from collections by the exploratory fishing vessel *Oregon* in the Gulf of Mexico and adjacent seas 1950 through 1955.—Special Scientific Report of the U.S. Fisheries and Wildlife Services—Fisheries 196:1–134.

Van Dam, A. J. 1933. Die Decapoden der Siboga-Expedition. VIII. Galatheidea: Chirostylidae. Siboga-Expeditie 39 a7:1–46.

(ALR) Institute of Oceanographic Sciences Deacon Laboratory, Wormley, Godalming, Surrey, GU8 5UB, United Kingdom; (JEM) Former address: Harbor Branch Oceanographic Institution, Inc., 5600 Old Dixie Highway, Fort Pierce, Florida 34946.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 309–316

PROCAMBARUS (GIRARDIELLA) STEIGMANI, A NEW CRAYFISH (DECAPODA: CAMBARIDAE) FROM A LONG-GRASS PRAIRIE IN NORTHEASTERN TEXAS

Horton H. Hobbs, Jr.

Abstract.—*Procambarus* (*Girardiella*) *steigmani,* a crayfish which appears to be a habitual (primary) burrower, is described from a single locality on the Parkhill Prairie, in the Trinity River watershed of Collin County, Texas. Its closest relative, from which it differs in possessing asymmetrical first pleopods in the male and a highly sculptured annulus ventralis in the female, is *P.* (*G.*) *regalis* which has been reported from the Ouachita and Red river basins of southwestern Arkansas.

Described herein is *Procambarus* (*G.*) *steigmani,* the third previously undescribed member of the subgenus *Girardiella* to be recognized since Hobbs & Robison (1988) reviewed the occurrence of the genus in Arkansas and presented a key and illustrations to aid in the recognition of the 10 then-known members of the *gracilis* group of the subgenus. *Procambarus* (*G.*) *kensleyi* and *P.* (*G.*) *nigrocinctus,* both rather distantly related to *P.* (*G.*) *steigmani,* were subsequently described by Hobbs (1990) from the Neches River basin of eastern Texas. The new species is closely allied to *P.* (*G.*) *regalis* Hobbs & Robison, 1988, from southwestern Arkansas, sharing so many features in common with that species that I am tempted to recognize it as a subspecies of the latter. Until more is known about the ranges of the two, the treatment proposed here seems to me, however, to be based on fewer assumptions.

An error is present in the key mentioned above (Hobbs & Robison 1988:404): at the end of couplet 2, "6" should read "7" and, at the end of couplet 5, "6" should replace "7." Using this key with the corrections noted, *P.* (*G.*) *steigmani* would be identified as *P.* (*G.*) *regalis* from which it may be distinguished readily by its possessing asymmetrical first pleopods, a feature apparently unique in the subgenus.

Procambarus (*Giradiella*) *steigmani,* new species
Figs. 1, 2

Crayfish.—Eig, 1990:1A, 5A, unnumbered color photograph.

Diagnosis.—Body pigmented, eyes well developed. Rostrum lacking marginal spines, tubercles, and median carina. Carapace without cervical spines or tubercles. Areola often linear but never less than 45.5 times as long as wide and constituting 37.4 to 41.9 ($\bar{X}$ = 40.1) % of total length of carapace (44.6 to 47.6, $\bar{X}$ = 46.0% of postorbital carapace length). Suborbital angle weak and obtuse. Hepatic and mandibular areas weakly tuberculate; branchiostegal spine absent. Antennal scale about 2.4 times as long as broad, widest distal to midlength. Ventral surface of palm of chela punctate mesially and laterally (rarely with single small tubercle ventromesially), no tubercles on ventral surface of dactyl. Ischium of third pereiopod of first form male with simple strong hook overreaching basioischial articulation; hook not opposed by tubercle on corresponding basis; coxa of fourth pereio-

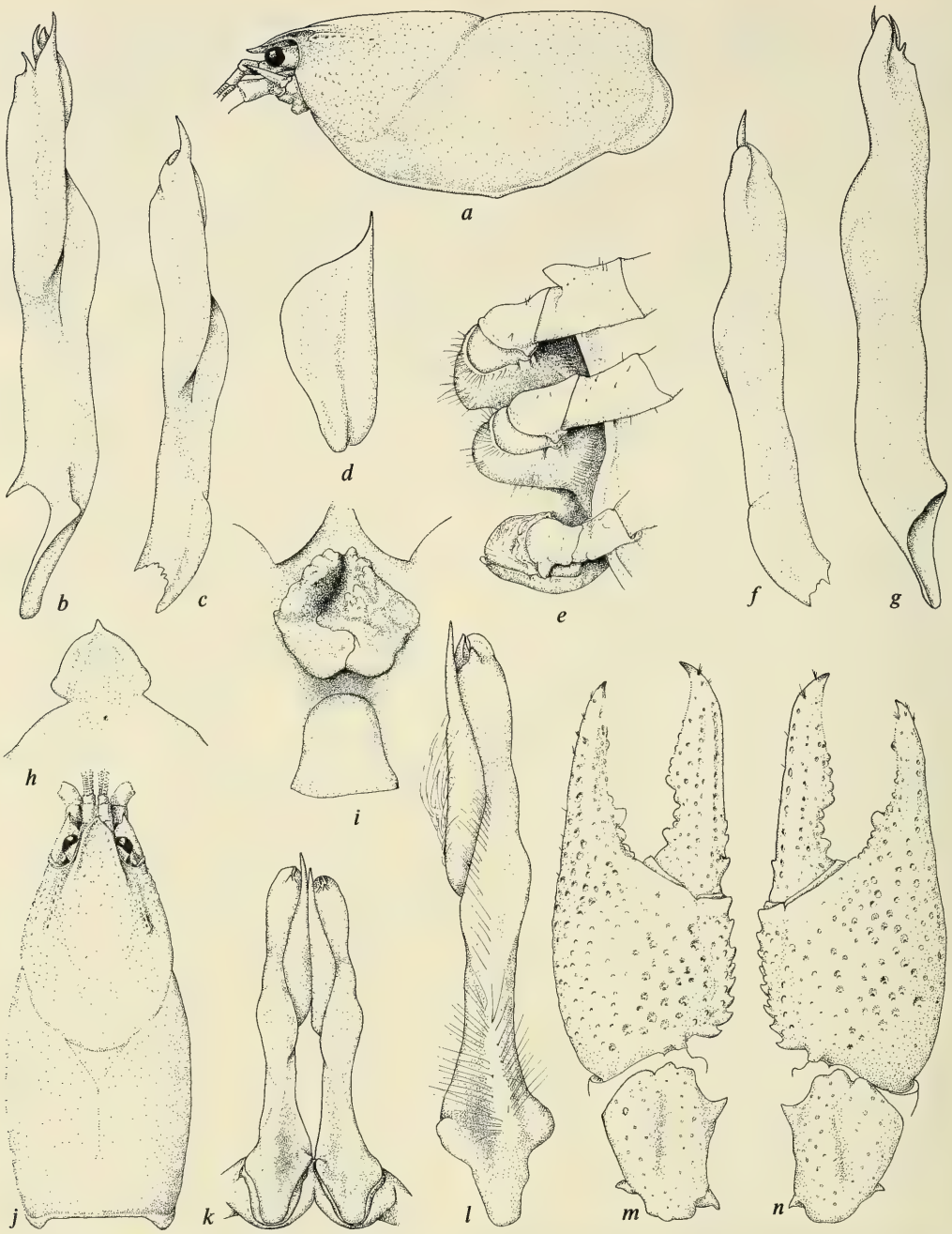


Fig. 1. *Procambarus* (*Girardiella*) *steigmani,* new species (holotype except c, f from morphotype, and i, m from allotype): a, Lateral view of carapace; b, c, Mesial view of first pleopod; d, Antennal scale; e, Basal podomeres of third, fourth, and fifth pereiopods; f, g, Lateral view of first pleopod; h, Cephalomedian lobe of epistome; i, Annulus ventralis and adjacent sternites; j, Dorsal view of carapace; k, l, Caudal view of first pleopods; m, n, Dorsal view of distal podomeres of cheliped.

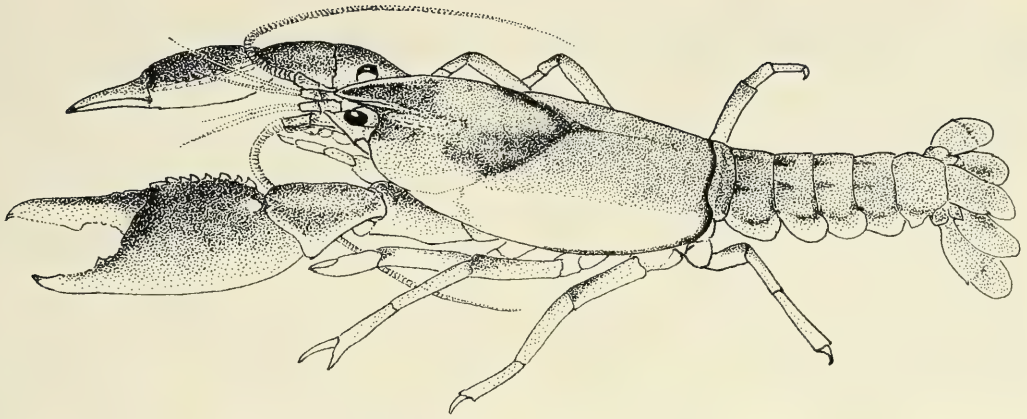


Fig. 2. Dorsolateral view of paratypic male, form I, *Procambarus* (*Girardiella*) *steigmani,* new species, illustrating color pattern.

pod lacking caudomesial boss. First pleopods of first form male reaching coxae of third pereiopods, asymmetrical, bearing tuberculiform proximomesial spur, angular sloping shoulder at base of terminal elements, and lacking subterminal setae; terminal elements, all at least partly sclerotized, consisting of: (1) straight to slightly curved, spiculiform mesial process overreaching other terminal elements; (2) short, acute, cephalodistally directed cephalic process situated at cephalolateral base of mesial process; (3) strong cornified obliquely flattened and caudodistally directed central projection; and (4) caudal element consisting of rounded, obliquely disposed, lamelliform lobe with mesiodistal angle and small, adnate, thumb-like lobe on caudomesial base of latter. Central projection slightly overreaching caudal element. Female with annulus ventralis freely movable, slightly broader than long, subsymmetrical in outline; deep cephalomedian trough leading to sigmoid sinus ending on caudal wall of annulus; anterolateral prominences highly sculptured and bearing prominent tubercles. Preannular plate obscure; postannular sclerite weakly tapering anteriorly and with anterior third sloping conspicuously dorsally; first pleopods present.

Holotypic male, form I.—Cephalothorax (Figs. 1a, j, 2) subovate, compressed laterally. Second abdominal segment narrower than thorax. Areola linear along most of its length. Cephalic section of carapace 1.2 times as long as areola, latter comprising 41.9% of total length of carapace (47.4% of postorbital carapace length). Surface of carapace smooth to punctate dorsally, weakly granulate ventrolaterally and sparsely tuberculate in hepatic and mandibular regions. Rostrum with thickened margins tapering from broad base to short acumen, latter indistinctly delimited basally; slightly upturned tip of acumen reaching midlength of penultimate podomere of antennular peduncle; dorsal surface concave anteriorly becoming subplane toward base and with few conspicuous punctations between those on mesial flank of ridges; subrostral ridges moderately prominent and evident in dorsal aspect to base of acumen. Postorbital ridges prominent, swollen posteriorly, deeply grooved laterally but weakly elevated dorsally, and lacking spines and tubercles. Paired posterior gastric prominences moderately conspicuous. Suborbital angle obtuse. Branchiostegal and cervical spines lacking.

Abdomen shorter than carapace. Pleura of third through fifth segments broadly rounded ventrally. Cephalic section of telson with 2 spines on right (3 on left) caudolateral corner, more lateral one on both

sides immovable. Cephalic lobe of epistome (Fig. 1h) campanulate in outline with small apical projection; elevated margins thickened, median area subplane; main body of epistome with fovea; epistomal zygoma arched. Ventral surface of proximal podomere of antennular peduncle with strong spine near midlength. Antennal peduncle lacking spines and prominent tubercles on three proximal podomeres; flagella broken but reaching second abdominal tergum in morphotype. Antennal scale (Fig. 1d) 2.4 times as long as wide, broadest distal to midlength; greatest width of lamellar area about twice that of thickened lateral part.

Third maxilliped extending anteriorly to level of ultimate podomere of antennule; ventral surface moderately setose, setae on mesial half of ischium and row on ventral surface of merus conspicuous, those extending mesially from sublateral row smaller and fewer in number; merus not completely obscured by setae in lateral aspect.

Right chela (Fig. 1n) subovate in cross section, depressed; width of palm 1.3 times length of mesial margin; latter slightly greater than ⅓ length of chela; except mesially and dorsomesially, palm mostly punctate although dark coloration of small, recessed tubercles over much of dorsolateral surface presenting erroneous first impression of its being strongly tuberculate. Mesial surface of palm with row of 7 cream-colored tubercles flanked dorsolaterally by irregular row of 8 almost black ones, and arc of 6 dark ones situated more laterally; no tubercles present on ventral flank of mesialmost row. Both fingers with poorly defined median longitudinal ridges dorsally and ventrally; ridges made evident largely by bordering punctuations. Opposable margin of fixed finger with row of 5 (4 on left) tubercles (distalmost largest on finger) on proximal fourth of finger, followed by row of 4 (3 on left) small ones along middle third, and abraded, more ventral, large one at base of distal fourth of finger; single row of minute denticles extending from largest tubercle to base of corneous tip of finger; lateral surface of finger rounded and bearing row of setiferous punctations. Opposable margin of dactyl with distinct excision at base supporting row of 3 tubercles followed by row of 5 in antepenultimate fourth of finger, single row of minute denticles present between and distal to latter row; mesial surface of finger with 2 (left with row of 3) tubercles near base followed by row of setiferous punctations.

Carpus of cheliped longer than broad with oblique furrow dorsally; mesial surface with 1 large, conical, corneous tubercle and 2 rudimentary ones proximal to it; dorsomesial distal angle corneous, dorsal surface punctate; ventromesial surface with arc of 3 tubercles leading to more mesial one of 2 situated on ventrodistal margin of podomere.

Merus of cheliped with 2 oblique dorsal rows of 3 tubercles each, two distalmost members larger than others and subacute; dorsomesial distal margin produced in conspicuous, weakly scalloped prominence; ventral surface with mesial row of 12 tubercles and lateral one of 6, only 1 or 2 tubercles not in linear series. Ischium with 1 (2 on left) tubercle ventromesially.

Hook on ischium of third pereiopod (Fig. 1e) simple, robust, overreaching basioischial articulation, and not opposed by tubercle on corresponding basis. Coxae of fourth and fifth pereiopods without caudomesial boss, mesial caudoventral angle of that of fifth with prominent tubercle.

Sternum between third, fourth, and fifth pereiopods comparatively shallow; ventrolateral margins with plumose setae obscuring much of first pleopods.

First pleopods (Fig. 1b, g, k, l) as described in "Diagnosis." Setae at caudal base splayed as in *Procambarus* (*G.*) *regalis.*

Uropods with mesial lobe of basal podomere produced in distally projecting spine; mesial ramus with distomedian spine small and premarginal; distolateral spine present on mesial and lateral rami.

Allotypic female.—Differing from holotype, other than in secondary sexual fea-

tures, in following respects: tubercles in hepatic and mandibular regions not numerous but conspicuous; anterior extremity of rostrum rounded, not forming apical prominence; dorsal surface of rostrum concave posteriorly to base, subrostral ridges evident in dorsal aspect to base of apical curvature; postorbital ridges terminating anteriorly in minute corneous tubercles; very small branchiostegal spine present on right side; 2 or 3 tubercles present in position occupied by cervical spines in many crayfishes; cephalic section of telson with 2 spines in each caudolateral corner; (right chela regenerated exemplifying usual short mesial margin of palm and comparatively straight opposable margins of fingers) left chela (Fig. 1m) with opposable margin of fixed finger like that of left member in holotype; opposable margin of dactyl of chela with additional tubercle situated opposite distal, more ventral one on fixed finger; mesial surface of carpus of cheliped with small tubercle at proximoventral base of large tubercle; prominence on distal dorsomesial margin of merus with 2 distinct scallops; dorsal surface of merus with 8 tubercles, only 1 of which conspicuously larger than others. For measurements see Table 1.

Table 1.—Measurements (in mm) of the primary types of *Procambarus* (*G.*) *steigmani*, new species.

	Holotype	Allotype	Morphotype
Carapace:			
Entire length	28.4	32.9	24.2
Postorbital length	25.1	28.9	21.2
Width	12.8	14.9	10.6
Height	13.1	14.6	11.0
Areola:			
Width	linear	linear	linear
Length	11.9	13.4	9.5
Rostrum:			
Width	4.3	4.5	3.3
Length	4.4	4.7	3.8
Chela:			
Length, palm mesial margin	7.7	7.8	6.7
Palm width	10.2	10.0	7.1
Length, lateral margin	22.2	22.0	15.3
Dactyl length	13.0	13.2	9.1
Abdomen:			
Width, second segment	9.7	11.6	9.1
Length, total	25.9	28.9	21.4

Annulus ventralis (Fig. 1i) as described in "Diagnosis." Preannular plate membranous, not clearly delimited posteriorly; postannular sclerite broad basally, gradually tapering anteriorly with apical third sloping conspicuously dorsally and when pressed against annulus foreshortened so that anterior margin appearing broadly rounded. First pleopods comparatively well developed, reaching at least midlength of annulus when abdomen flexed.

Morphotypic male, form II.—Differing from holotype in following respects: areola shorter, constituting only 39.3% of carapace length; apex of acumen almost reaching distal margin of penultimate podomere of antennular peduncle; branchiostegal spines and cervical tubercles weak; cephalic section of telson with 2 spines in each caudolateral corner; cephalomedian projection of epistome minute; 8 tubercles in mesialmost row on mesial surface of palm, 6 in adjacent row, and 5 or 6 in more lateral curved row; dorsal longitudinal ridge well defined on dactyl; tubercle count on opposable margin of fixed finger 3 and 6 on right (tubercles abraded on left), 3 and 4 on that of dactyl of left chela (probably also on damaged right); dorsal distomedian angle of carpus produced in short spine, and 2 small spines between mesial and ventromesial spines; tubercles on dorsomesial distal prominence of merus more clearly defined. Hook on ischium of third pereiopod very weak, not nearly reaching basioischial articulation; tubercle on ventral caudomesial angle of coxa of fifth pereiopod reduced in size. First pleopod (Fig. 1c, f) with less conspicuous shoulder on cephalic surface, stouter mesial process, cephalic process not differentiated from poor-

ly defined processes of central projection, and lamella and thumb-like parts of caudal element less distinctly defined.

Color notes.—Holotype (Fig. 2): Dominant colors cherry red and pale blue. Carapace cherry red dorsally, slightly paler from posterior level of postorbital ridges anteriorly; ridges, lateral rostral carinae, and paired spots on posterior gastric region vermilion. Cervical groove and mandibular adductor areas dark reddish brown. Orbital region dark brown suffused with red; hepatic region dark red dorsally quickly fading anteroventrally to pink, lavender, and over antennal and mandibular regions very pale blue. Branchiostegites with dorsal red area sharply set off from lateral pale blue region along line from level of site usually occupied by cervical tubercle to dorsal end of caudal flange. Marginal ridge, caudal flange, and caudal ridge dark bluish gray. Dorsal surface of abdomen slightly paler red than posterior dorsum of carapace; second through fifth terga with paired dark purplish red, caudally-divergent spots dorsolaterally. Lateral limits of same terga marked by arched paler purplish red marks abutting pink pleura. Telson and uropods red, rami of latter with red fading toward borders; dark splotch situated caudomesially on mesial rami. Dorsum of merus and carpus of cheliped reddish brown with bluish to lavender blush; carpus with large distomesial spine and distomesial angle pinkish cream. Dorsal surface of palm of chela tan; area flanking base of dactyl darkened by bluish suffusion; most tubercles and punctations very dark, but proximodorsal articular condyle and mesialmost row of tubercles on palm pinkish cream. Both fingers pale blue with cream on proximal flank of corneous tips. Remaining pereiopods pinkish cream with bluish suffusion on merus and carpus, darkest at junctions of these podomeres. Ventral surface of all pereiopods and abdomen cream with pinkish blush. Podomeres of antennae and antennules cream to pale tan; flagella pale olive. Third maxillipeds mostly pinkish cream.

The color pattern of the allotype is almost identical to that of the male, but the coloring differs markedly. Carapace with dorsum chocolate brown setting off tannish cream postorbital ridges and rostral carinae. Terga of abdomen reddish brown and pleura cream. Uropods and caudal section of telson pale pinkish tan, mesial ramus of uropods lacking dark caudomesial splotch. Pereiopods as in holotype except lacking pinkish suffusion. The morphotype bore the same coloration as the holotype; however, the reds were more subdued.

Size.—The largest specimen available is a first form male having a carapace length of 37.0 mm (postorbital length of 32.7 mm). The smallest first form male has corresponding lengths of 28.3 and 25.0 mm. Measurements are not available for either ovigerous females or ones carrying young; for those of the primary types, see Table 1.

Type locality.—Parkhill Prairie, a 52 acre tract of grassland in the Trinity River basin, 9.4 miles (15 km) north of U.S. Highway 380 off State Highway 36, Collin County, Texas (33°16′N, 96°18′W). The soil on the Prairie belongs to the Houston Series which consists of calcareous clays that here are shallowly to deeply eroded. Among the conspicuous grasses are *Andropogon gerardii, Schizachyrium scoparium, Tripsacum dactyloides, Sorghastrum nutans, Bouteloua curtipendula,* and *Panicum virgatum.* In the spring, the wildflowers include the Indian paintbrush, White winecup, and Wild petunia and, in the fall, Maximilian Sunflower, Ironweed, and asters. There this crayfish along with representatives of *Procambarus* (*Girardiella*) *curdi* Reimer, 1975, occupy burrows that descend to an unknown depth below the surface. The burrows are marked by turrets consisting of pellets of soil that when dry are light gray in color, contrasting sharply with the green to brown grass. In an account of the discovery of this crayfish by

Ken Steigman, Eig (1990) included a photograph of the Parkhill Prairie and another of what appears to be a female of *P.* (*G.*) *steigmani.*

Disposiiton of types.—The holotypic male, form I, allotype, and morphotypic male, form II, are deposited in the National Museum of Natural History, USNM 220525, 220526, and 220527, respectively, as are the paratypes consisting of 10 ♂ I, 5 ♂ II, and 12 ♀.

Range and specimens examined.—All of the specimens available were obtained by K. Steigman from snake traps set in the type locality. Thus, all were crawling among the grass when they wandered into the traps: 6 ♂ I, 5 ♂ II, and 12 ♀ were taken on 14 Feb 1990, 1 ♂ I on 28 Apr 1990, 2 ♂ I on 28 May 1990, and 1 ♂ I, date uncertain. In addition, the primary types were, among other specimens, perhaps lured into a trap during a dry spell in late June or early July (when 5 to 8 cm cracks penetrated a meter into the soil) by introducing into the trap water-soaked foam rubber in an open ziplock bag.

Variations.—All of the specimens that I have examined are from the same locality, and the variations noted among them are minor ones, many, if not most, associated with injury in earlier instars. The rostrum reaches anteriorly between the proximal ends of the penultimate and ultimate podomeres of the antennular peduncle. Branchiostegal spines, which at most are small, may be vestigial or lacking. Tubercles along the posterior flank of the cervical groove, one of which a probable homologue of the cervical spine, may or may not be present; the postorbital ridges may terminate anteriorly in a minute, corneous tubercle or may merge imperceptibly with the surface of the orbital area; the ridges are sometimes so depressed just posterior to midlength as to appear almost bipartite. The paired sclerotized knobs in the posterior gastric region are not always discernible. The mesial lobe of the proximal podomere of the uropod is not always produced into a spine; it may even be truncate. The most readily recognized variations occur in the number of tubercles on the several podomeres of the cheliped: the ventromesial surface of the ischium has 2 or 3; 6 to 8 tubercles occur in the dorsal surface of the merus where usually 2 are spiniform (rarely 1 or 3), the ventromesial row consists of 9 to 14 and the ventrolateral one of 4 to 7; the number of tubercles in the arc on the ventromesial surface of the carpus ranges from 0 to 4; the mesialmost row of tubercles on the palm of the chela consists of 6 to 8, 5 to 8 in the adjacent dorsolateral row, and 4 to 7 in the more lateral curved row; the opposable margin of the fixed finger exhibits 2 to 4 tubercles proximal to the first large tubercle and a continuing row of 4 to 6 more distally; the corresponding margin of the dactyl bears 3 or 4 in the basal concavity and 4 to 8 more distally, 1 to 3 tubercles are present on the proximomesial surface of the finger.

Relationships.—*Procambarus* (*G.*) *steigmani* has its closest affinities with *P.* (*G.*) *regalis* and, as suggested in the introductory remarks, may well prove to be a subspecies of the latter which is currently known only from the Ouachita and Red river basins of southwestern Arkansas (Hobbs & Robison 1988:fig. 15). The similarities between the two include almost identical terminal elements of the first pleopods in the male, thickened rostral margins, postorbital ridges that are swollen posteriorly, chelipeds that are markedly similar, and color patterns that also betray a close common ancestry. Features that seem most reliably to distinguish them are the following found in the new species: an asymmetrical arrangement of the first pleopods, the first recorded for a member of the subgenus *Girardiella*; the absence of tubercles on the ventral surface of the palm of the chela; the strongly tuberculate annulus ventralis, and the cherry red and pale blue coloration of the male and the

chocolate brown color noted in the female. Should these colors prove to be typical of the species they will furnish a ready diagnostic character for recognition of the crayfish in the field. In *P.* (*G.*) *regalis,* the pleopods of the male are always symmetrically situated; at least a few tubercles are always present on the ventral surface of the palm of the chela, and in only one specimen [collected 1.5 mi (2.4 km) N of Paraloma, Sevier County, Arkansas] that I have examined do the anterolateral prominences of the annulus approach the tuberculate condition that appears to be typical of *P.* (*G.*) *steigmani.* The colors of the carapace of *P.* (*G.*) *regalis* as recorded by Hobbs & Robison (1988) are brownish red and tannish cream, not nearly so brightly colored as are the males of the new species.

Etymology.—It is a pleasure to name this crayfish in honor of its discoverer, Ken Steigman.

Acknowledgments

Thanks are extended to K. Steigman of the Heard Natural Science Museum and Wildlife Sanctuary, McKinney, Texas, for providing me with the specimens on which this description is based and for information concerning the type locality and the few habits of the crayfish reported here. Appreciation is also extended to J. F. Fitzpatrick, Jr., of the University of South Alabama, H. H. Hobbs III of Wittenberg University, and my colleague T. E. Bowman for their comments on a draft of this manuscript.

Literature Cited

Eig, Jonathan. 1990. Mud boggling.—The Dallas Morning News, Saturday, July 21, 1990, pp. 1A, 5A.

Hobbs, H. H., Jr. 1990. On the crayfishes (Decapoda: Cambaridae) of the Neches River basin of eastern Texas with the descriptions of three new species.—Proceedings of the Biological Society of Washington 103:573–597.

———, & H. W. Robison. 1988. The crayfish subgenus *Girardiella* (Decapoda: Cambaridae) in Arkansas, with the descriptions of two new species and a key to the members of the *gracilis* group of the genus *Procambarus.*—Proceedings of the Biological Society of Washington 101: 391–413.

Reimer, R. D. 1975. *Procambarus* (*Girardiella*) *curdi,* a new crawfish from Arkansas, Oklahoma, and Texas (Decapoda, Astacidae).—Tulane Studies in Zoology and Botany 19(1 & 2):22–25.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 317–321

A NEW SPECIES OF *PROCESSA* FROM BERMUDA (CRUSTACEA: DECAPODA: CARIDEA)

Raymond B. Manning and C. W. Hart, Jr.

Abstract.—*Processa famelica,* the tenth western Atlantic species of *Processa* to be recognized and the third species to be named from Bermuda, is described from material collected at Hungry Bay, Bermuda. It can be distinguished from all American congeners by its elongate rostrum, which extends beyond the eye.

Two species of *Processa* have been described from localities in Bermuda, and, until now, these were the only two species known to occur there. *Processa bermudensis* (Rankin, 1900) was described from material collected in Harrington Sound and was redescribed from Bermudan material by Gurney (1936:624). It subsequently has been recorded from localities between North Carolina and Brazil (Manning & Chace 1971, Christoffersen 1979, Williams 1984). *Processa wheeleri* Lebour, 1941, still known only from the type material, was described from material taken while night dredging in Ferry Reach.

The species described below was collected in Hungry Bay in 1979 and 1980 during visits to Bermuda to study Bermudan cave shrimps, a project sponsored by the Smithsonian under its Scholarly Studies Program.

All specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The abbreviation cl is used for postorbital carapace length.

Processa famelica, new species
Figs. 1–3

Material.—Hungry Bay, Bermuda [32°17′N, 64°46′W]: 1 ♂, cl 5.0 mm (holotype, USNM 252202), 16 Nov 1979, leg. R. B. Manning.—1 ♂, cl 4.8 mm, 2 ovigerous ♀, cl 5.8–7.0 mm (paratypes, USNM 252226), 13 May 1980, leg. R. B. Manning and C. W. Hart, Jr.

Diagnosis.—Rostrum extending beyond eyes. Antennal spine present. Stylocerite unarmed. Second pereopods asymmetrical: larger right with 15–18 meral and 26–30 carpal articles, smaller left with 5–6 meral and 13–15 carpal articles. Carpus of fifth leg slightly longer than propodus. Abdominal sternites unarmed. Fifth abdominal somite unarmed posterolaterally. Lobe on sixth abdominal somite above articulation of uropod unarmed.

Description.—Rostrum deflexed, extending beyond anterior edge of eye; apex bifid, lower tooth larger. Lower orbital angle low, rounded. Antennal spine present. Lower anterior angle of carapace broadly rounded.

Abdomen smooth. Fifth abdominal somite rounded posterolaterally. Sixth abdominal somite about as long as fifth, bluntly angled posterolaterally; lateral plate of sixth abdominal somite unarmed.

Telson about 1.5 times longer than sixth abdominal somite, length about 3 times greatest width, with 2 pairs of dorsal and 2 pairs of distal spines; anterior pair of dorsal spines set in anterior fourth, posterior pair beyond midlength; distance between anterior margin and anterior pair of dorsal spines about ⅓ distance between pairs of dorsal spines; inner of distal spines stronger; apex of telson acutely pointed.

Eye moderately large, cornea width subequal to length of stalk and cornea combined, slightly more than 2 times greatest width of antennal scale.

Antennular peduncle extending beyond

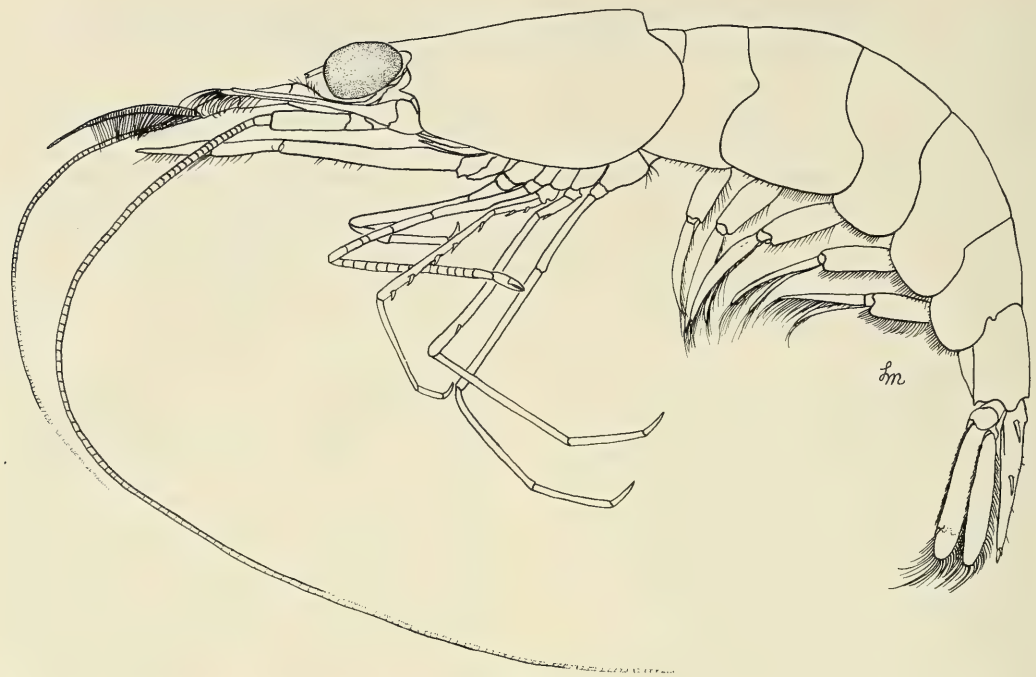


Fig. 1. *Processa famelica,* new species, male, cl 5.0 mm, lateral view.

rostrum by distal 2 segments and about ¼ of proximal segment, latter slightly longer than distal segments combined; ultimate segment more than half as long as penultimate segment; proximal segment with ventral spine, set slightly beyond midlength. Stylocerite obtusely rounded laterally, unarmed, inner margin extending further anteriorly than outer. Dorsolateral flagellum of antennule about half as long as carapace; ventromesial flagellum about twice as long as carapace.

Antennal scale extending to or almost to end of antennular peduncle, length of scale about 5 times greatest breadth; broad distal spine of scale not overreaching blade. Antennal peduncle extending about to middle of second segment of antennular peduncle. Basal segment of antenna lacking ventrolateral spine. Antennal flagellum about 4 times as long as carapace.

Third maxilliped overreaching antennal scale by half of distal segment; ultimate segment about as long as penultimate, apex acute; exopod well developed. Other mouthparts as figured by Manning & Chace (1971) for species of *Processa.*

First pereopods not extending to end of antennal scale. Right first pereopod chelate; fingers about ⅔ length of palm; carpus shorter than palm; merus longer than carpus and chela combined. Left first pereopod with simple dactyl, about ⅓ as long as propodus; carpus about ¾ as long as propodus; merus as long as distal segments combined.

Second pereopods unequal, right longer, overreaching antennal scale with chela, merocarpal articulation not extending to end of scale; ischium with 3–5 indistinct, merus with 15–18, and carpus with 26–30 articles; fingers more than half as long as palm; carpus about 5 times as long as chela, merus 3 times as long as chela; ischium subequal to merus. Left second pereopod over-reaching antennal scale with part of carpus and all of chela, merocarpal articulation not extend-

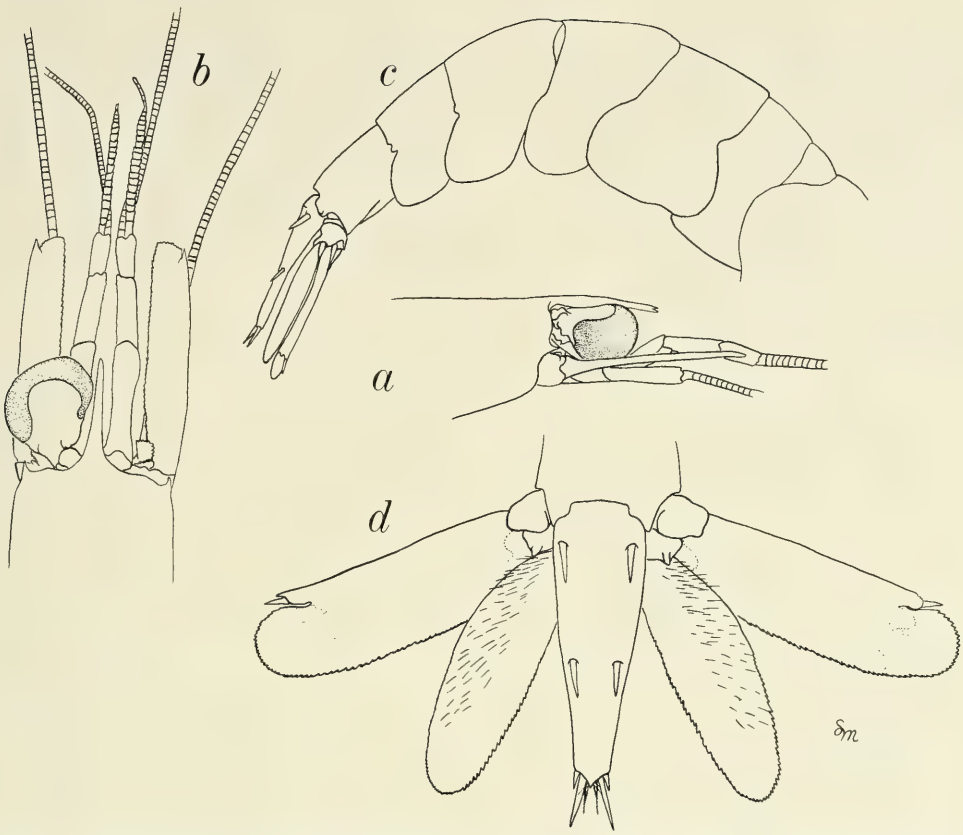


Fig. 2. *Processa famelica,* new species, male, cl 5.0 mm: a, front, lateral view; b, front, dorsal view; c, abdomen and telson, lateral view; d, tail fan, dorsal view.

ing to cornea; ischium undivided, merus with 5–6 and carpus with 13–15 articles; fingers shorter than palm; carpus slightly more than 4 times as long as chela; merus 3 times as long as chela; ischium about as long as merus.

Third pereopod overreaching antennal scale with part of carpus and all of propodus and dactyl; dactyl slender, simple; propodus about 3 times as long as dactyl, unarmed; carpus slightly more than twice as long as propodus, unarmed; merus about twice as long as propodus, about as long as carpus, with 5 movable spines on outer surface; ischium about ⅔ as long as merus, with 2 movable spines; combined length of propodus and carpus of third leg slightly less than length of ischium and merus.

Fourth pereopod overreaching antennal scale with distal end of propodus and dactyl; dactyl slender, simple; propodus 2.5 times as long as dactyl, unarmed; carpus more than twice as long as propodus, unarmed; merus twice as long as propodus, with 5 movable spines on outer surface; ischium less than half as long as merus, with 2 movable spines; combined length of carpus and propodus of fourth leg subequal to combined length of ischium and merus.

Fifth pereopod overreaching antennal scale with propodus and dactyl; dactyl slender, simple; propodus about 2.5 times as long as dactyl, unarmed; carpus about 1.5 times as long as propodus, unarmed; merus slightly longer than propodus, unarmed; ischium less than half as long as merus, un-

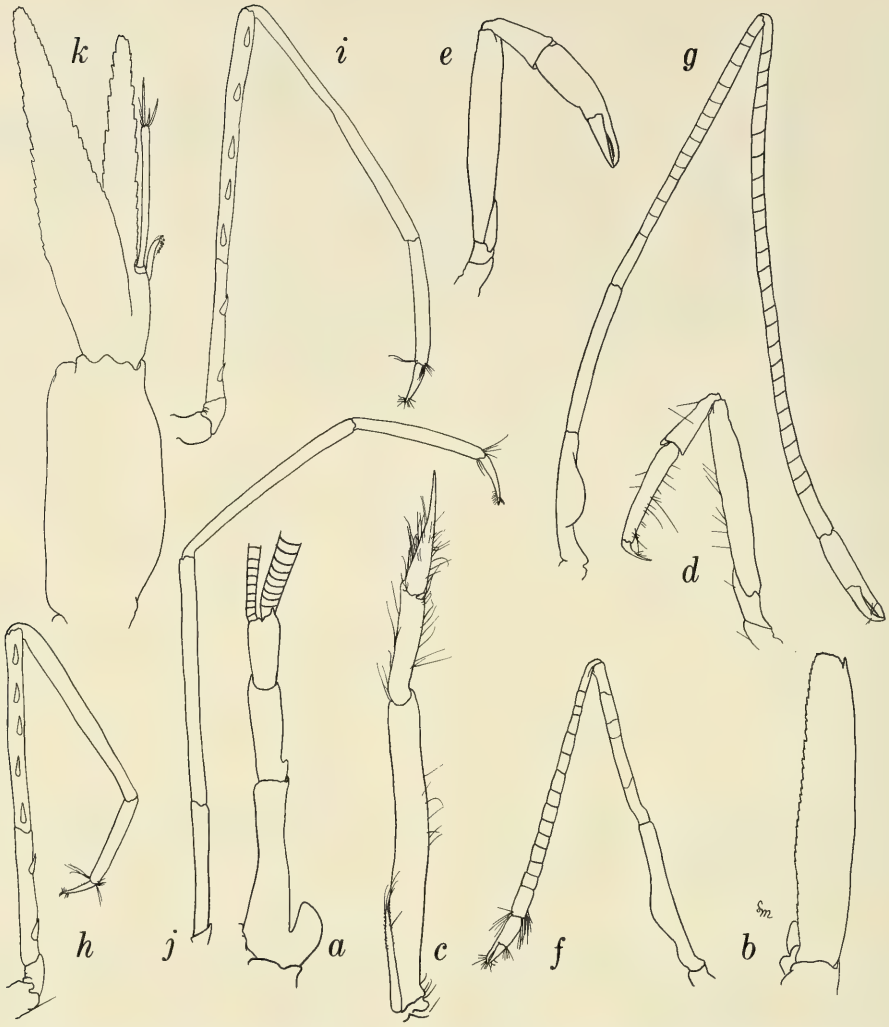


Fig. 3. *Processa famelica* new species, male, cl 5.0 mm: a, antennular peduncle; b, antennal scale; c, third maxilliped; d, left first pereopod; e, right first pereopod; f, left second pereopod; g, right second pereopod; h, left third pereopod; i, left fourth pereopod; j, left fifth pereopod; k, left second pleopod.

armed; combined length of propodus and carpus of fifth leg slightly less than combined length of ischium and merus.

Abdominal sternites unarmed.

Outer margin of uropodal exopod terminating in triangular spine, with longer, slenderer mesial spine; suture distinct. Endopod surface sparsely setose.

Ova small and numerous, eyed ova 0.4–0.6 mm in diameter.

Size.—Carapace lengths of males 4.8 and 5.0 mm, of ovigerous females 5.8 and 7.0 mm.

Name.—The specific name is from the Latin, *famelicus,* hungry, alluding to its occurrence in Hungry Bay.

Remarks.—*Processa famelica* is unique among western Atlantic species in having a rostrum that extends beyond the eyes. Although similar to *P. bermudensis* and *P.*

wheeleri, this new species differs from the former in having an internal spine and from the latter in having the stylocerite unarmed.

Processa famelica resembles the eastern Atlantic *P. elegantula* Nouvel & Holthuis, 1957 in having the long rostrum extending beyond the eyes but in that species the stylocerite is armed with a strong outer spine and the outer spine of the antennal scale overreaches the blade.

This new species was collected during the day on clean sand in shallow water, depth less than 0.5 meter, while sampling burrow openings of infaunal organisms with a yabby pump (Manning 1975). It was not taken together with any other species, but it is likely that it, like the species of *Ambidexter* reported by Abele (1972) and Williamson (1980), lives in the burrow of another invertebrate, either an annelid worm or a callianassid shrimp.

Based on her work with larvae, Lebour (1941:302) remarked that "There must be at least three, and probably four, species of *Processa* in Bermudan waters," suggesting that another species might exist there.

Literature Cited

Abele, L. G. 1972. A review of the genus *Ambidexter* (Crustacea: Decapoda: Processidae) in Panama.—Bulletin of Marine Science 22(2):365–380.

Christoffersen, M. L. 1979. Decapod Crustacea: Alpheoida. Campagne de la *Calypso* au large des côtes Atlantiques de l'Amérique du Sud (1961–1962), I.—Résultats Scientifiques des Campagnes de la *Calypso* 11:297–377.

Gurney, R. R. 1936. A description of *Processa bermudensis* Rankin and its larvae, IV. Notes on some decapod Crustacea of Bermuda, III–IV.—Proceedings of the Zoological Society of London (series B, part 1) 1936:621–630, pls. 1–7.

Lebour, M. V. 1941. Notes on thalassinid and processid larvae (Crustacea Decapoda) from Bermuda.—Annals and Magazine of Natural History (series 11) 7:401–420.

Manning, R. B. 1975. Two methods for collecting decapods in shallow water.—Crustaceana 29: 317–319.

———, & F. A. Chace, Jr. 1971. Shrimps of the family Processidae from the northwestern Atlantic Ocean (Crustacea: Decapoda: Caridea).—Smithsonian Contributions to Zoology 89:1–41.

Nouvel, H., & L. B. Holthuis. 1957. Les Processidae (Crustacea Decapoda Natantia) des eaux européennes.—Zoologische Verhandelingen, Leiden 32:1–53, figs. 1–220.

Rankin, W. M. 1900. The Crustacea of the Bermuda Islands, with notes on the collections made by the New York University Expeditions in 1897 and 1898.—Annals of the New York Academy of Sciences 12(12):521–548, pl. 17.

Williams, A. B. 1984. Shrimps, lobsters and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, xviii + 550 pp.

Williamson, D. I. 1980. Larval development in a species of *Ambidexter* Manning & Chace (Decapoda, Caridea, Processidae).—Crustaceana 39: 235–246.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 322–327

A NEW GENUS AND SPECIES OF NEOTROPICAL WATER BEETLE, *JOLYELMIS AUYANA,* FROM A VENEZUELAN TEPUI (COLEOPTERA: ELMIDAE)

Paul J. Spangler and Robin A. Faitoute

Abstract.—A new genus and species of the aquatic beetle family Elmidae, *Jolyelmis auyana,* is described and illustrated with pen and ink drawings and scanning electron micrographs. The biotope on Auyan-tepui, Bolivar, Venezuela, is described.

The distinctive new genus of elmid beetle described below was sent to us by Luis J. Joly, one of the collectors. Joly and A. Chacon collected specimens of this taxon from a cascade on Auyan-tepui in Bolivar, Venezuela. Auyan-tepui is the largest plateau (700 km^2) of the group of plateaus found in the ancient area of the Guayana Highland Shield of northern South America. These ancient plateaus are known to be inhabited by many endemic plants and animals. We describe this new genus so others may be aware of it and help establish its range and, eventually, determine whether it is or is not endemic to Auyan-tepui.

Elminae

Jolyelmis, new genus

Diagnosis.—This new genus may be distinguished from all other known elmid genera of the Western Hemisphere by the following combination of characters. Pronotum and each elytron with 3 high, longitudinal carinae (Figs. 2, 8); metasternum with an arcuate, lateral carina on each side of disc (Fig. 10); an arcuate carina extending from medial margin of each metacoxal cavity to posterior margin of abdominal sternum 1 (Fig. 14).

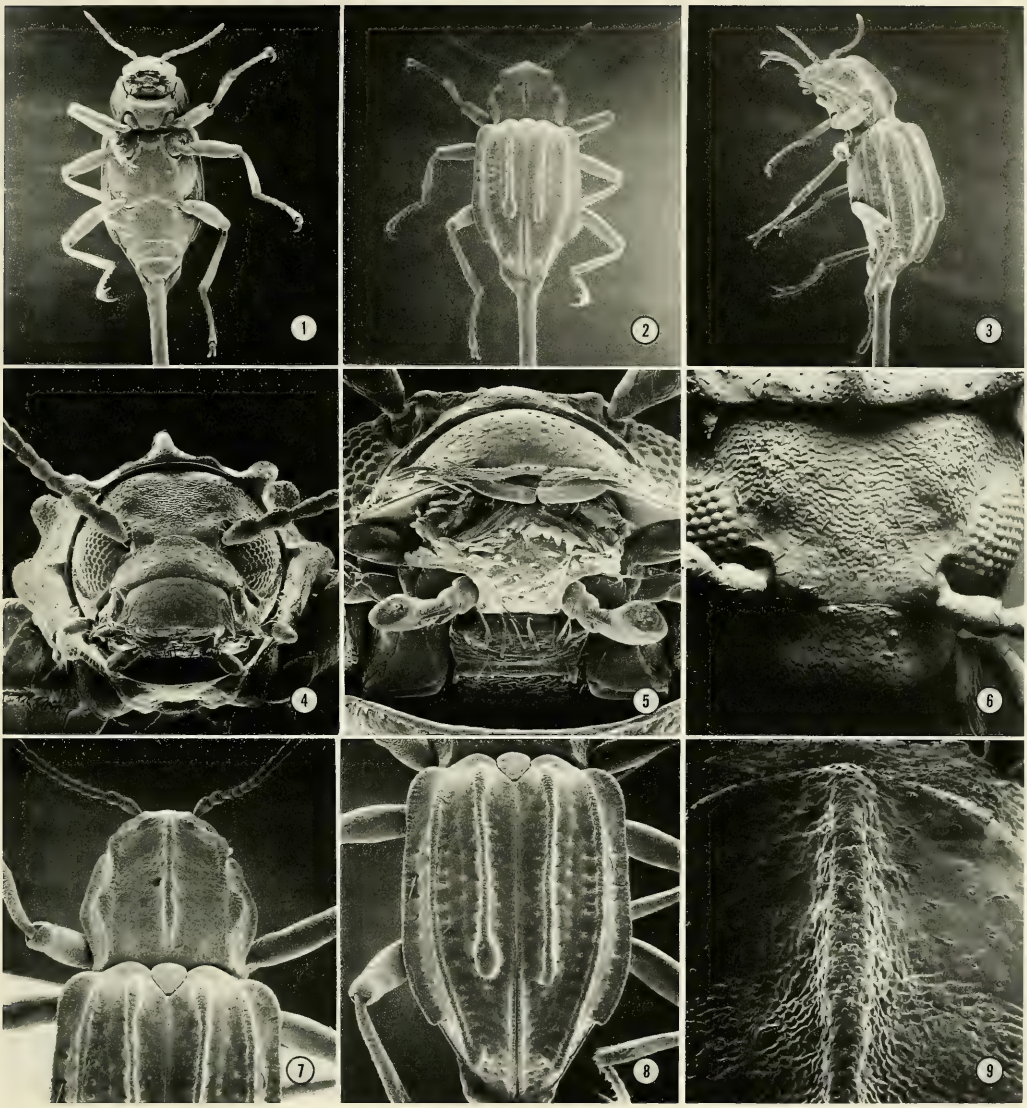
Description.—Body form subovate, convex dorsally (Figs. 1–3); pronotum about a third as long as elytron. Dorsal and ventral surfaces with very sparse, fine, golden setae. Tracts of thick golden plastron setae on gena, prosternum, hypomeron, epipleuron, proepisternum, mesepisternum, metepisternum, metasternum, abdominal segments 1–3, coxae and trochanters, profemora, mesofemora, and posterior (inner) surfaces of all femora. Cleaning fringe formula, 2-2-1.

Head retracted into pronotum. Antenna, 11 segmented. Labrum about twice as wide as long (Fig. 4); anterolateral margins moderately arcuately rounded. Clypeus transversely rectangular, about 3 times as wide as long (Fig. 4). Maxillary palpus, 4 segmented. Labial palpus, 3 segmented. Mentum transversely rectangular (Fig. 5). Submentum as wide as but a fifth as long as mentum (Fig. 5).

Pronotum subquadrate; widest at midlength (Fig. 7); sinuate/arcuate laterally; with 2 distinct, sublateral, bisinuate carinae; sublateral carinae extending entire length of pronotum, gibbose at three-fourths of its length, then narrower and lower at posterolateral corners; meson with an unevenly raised carina extending from anterior margin almost to base. Scutellum subtriangular (Fig. 15).

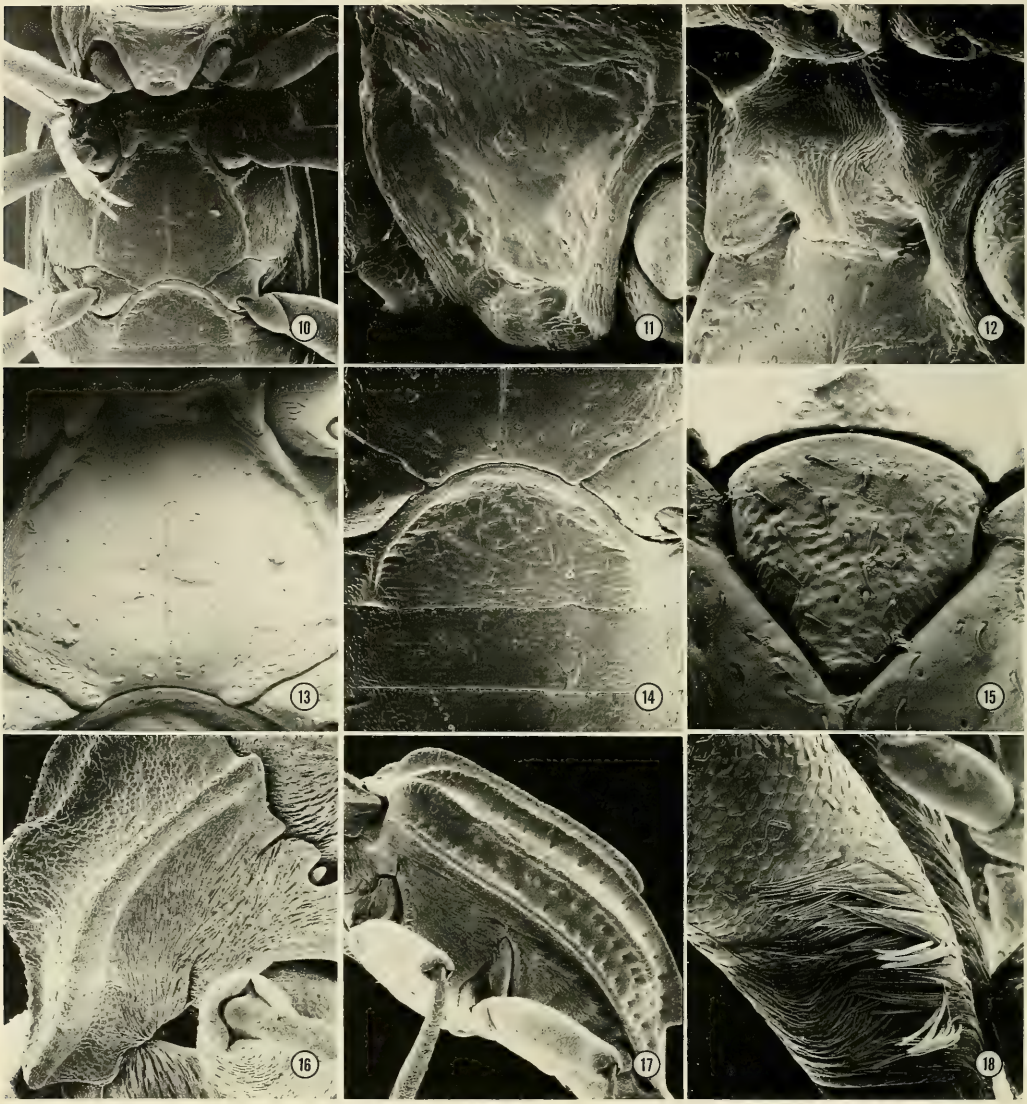
Elytron with 10 poorly defined, longitudinal rows of punctures and 3 high, evenly raised carinae of unequal length (Fig. 8). Innermost carina shortest, middle carina longest, lateral-most carina intermediate in length; all carinae terminate abruptly.

Prosternum broad, more than 4 times as



Figs. 1–9. *Jolyelmis auyana,* new genus, new species: 1, habitus, ventral view, ×35; 2, habitus, dorsal view, ×35; 3, habitus, lateral view, ×35; 4, head, adoral view, ×140; 5, labium and mouthparts, ×300; 6, vertex and clypeus, ×250; 7, head, pronotum and elytral bases, ×75; 8, elytra, ×75; 9, carina, pronotal meson, ×400.

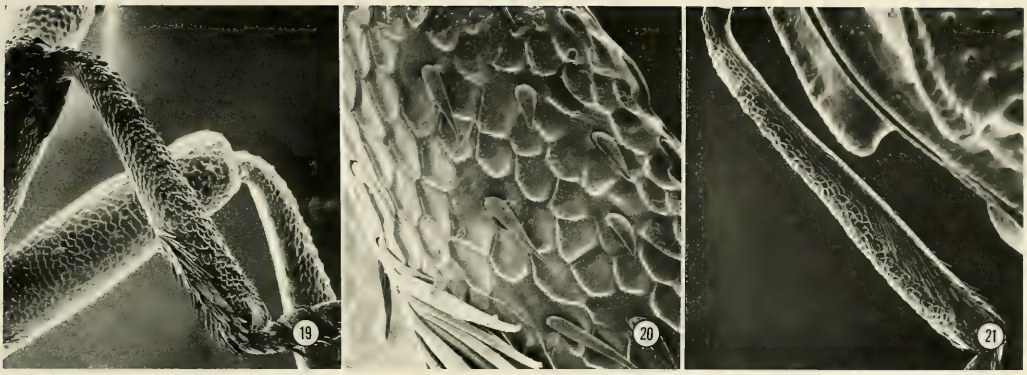
wide as width of procoxa; with transverse depression extending entire width just in front of procoxae (Fig. 10). Prosternal process broad, ending just behind procoxae (Fig. 10), slightly longer than prosternum in front of procoxae. Mesosternum with deep, broad, rimmed medial depression in front of and between anterior fourth of mesocoxae for reception of prosternal process; posterior margin with a deep fovea (Fig. 12) on each side of meson. Metasternum wider than long (Fig. 10); with 1 complete carina each side of disc, carinae extending from posteromedial edges of mesocoxae to middle of anterior edges of metacoxae; disc with narrow, shallow, longitudinal, mesal groove (Fig. 13); without plastron setae. Procoxae and mesocoxae rounded (Fig. 10). Metacoxae trans-



Figs. 10–18. *Jolyelmis auyana,* new genus, new species: 10, prosternum, mesosternum, metasternum, and abdominal sternum 1, ×100; 11, prosternal process, oblique view, ×400; 12, mesosternum, oblique view, ×350; 13, metasternal disc, ×220; 14, carina, abdominal sternum 1, ×220; 15, scutellum, ×550; 16, hypomeron, ×230; 17, epipleuron, ×100; 18, profemoral fringe, ×500.

verse (Fig. 10). Anterior and posterior surface of profemur (Fig. 18) and mesofemur with basal patch of long, dense, golden setae. Posterior surface of metafemur with basal patch of long, dense, golden setae. Protibiae (Fig. 19) and mesotibiae each with a cleaning fringe of golden setae on anterior and posterior surfaces. Metatibia with 1 apical cleaning fringe on posterior surface (Fig. 21). Tarsal claws robust, without teeth.

Abdomen with 5 visible, convex, evenly rounded sterna. Sterna not lobed laterally. Sternum 1 rimmed anteromedially; rim continuing laterally as arcuate carina; cari-



Figs. 19–21. *Jolyelmis auyana,* new genus, new species: 19, protibial cleaning fringe, ×220; 20, protibial sculpture, ×1300; 21, metatibial cleaning fringe, ×200.

nae extending from medial margin of metacoxal cavity almost to posterior margin of sternum 1 (Figs. 10, 14).

Type species.—*Jolyelmis auyana,* new species; gender feminine.

Etymology.—This genus is named for our friend Luis Jose Joly, one of the collectors of the type series.

Comparative notes.—This genus is a member of the subfamily Elminae and, unfortunately, there is no key to the 36 known neotropical elmid genera of the subfamily. For comparison, we have representatives of all of the described elmid genera of the Western Hemisphere and the distinctive exceptionally high carinae on the pronotum and elytra distinguish *Jolyelmis.*

Jolyelmis auyana, new species
Figs. 1–25

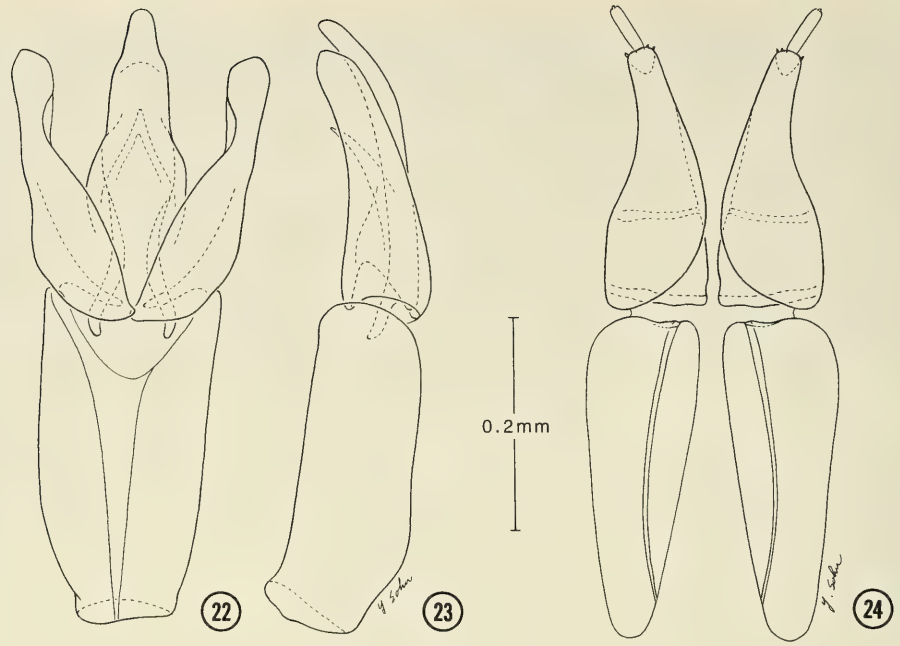
Holotype ♂.—Form and size: Oval. Length, 1.96 mm; width, at elytral midlength, 0.91 mm.

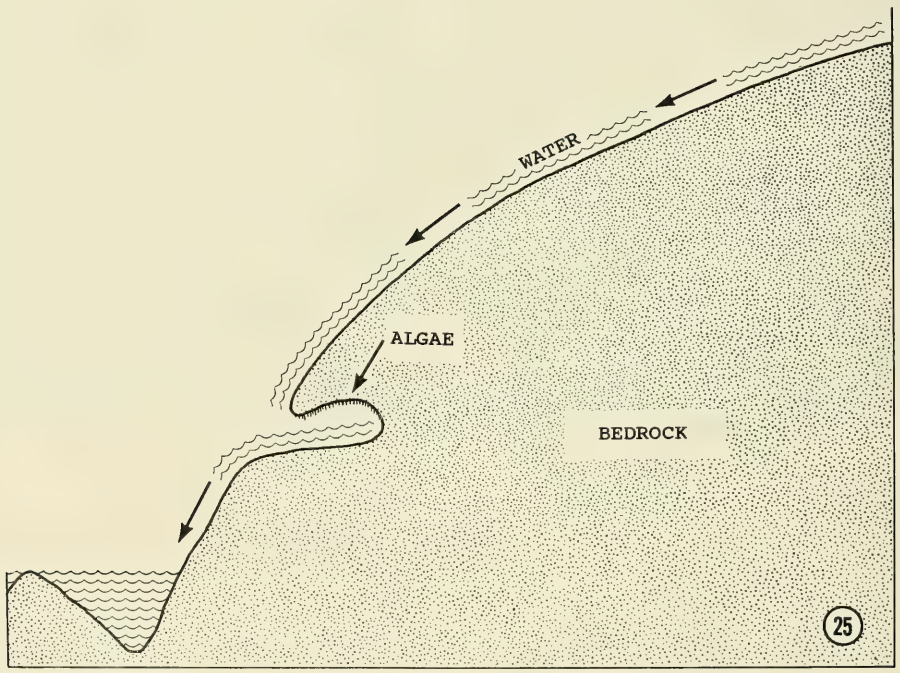
Color: Black except antennal segments 1 and 2 and maxillae reddish brown.

Plastron: Tracts of thick golden plastron setae on gena; sides of prosternum; hypomeron except small, anterior, slender carina (Fig. 16) and triangular wedge posteriorly; epipleuron posteriorly to abdominal segment 3 (Fig. 17); proepisternum; mesepisternum; metepisternum; lateral surfaces of metasternum and abdominal sterna 1–3 (Fig. 17); posterolateral surfaces of coxae and trochanters; basal third of anterior surface of profemora (Fig. 18); basal fourth of anterior surface of mesofemora; and basal third of posterior (inner) surfaces of all femora.

Head: Partially retracted into pronotum. Vertex with shallow, V-shaped depression behind antennal acetabula and between eyes (Fig. 6). Surface microreticulate; with sparse, fine setae. Antennal segments 1 and 2 slightly thicker than remainder; segment 3 as long as segment 2. Clypeus moderately arcuate apically (Fig. 4); nearly 3 times as wide as long. Clypeal and labral surfaces with fine, very sparse punctures and flattened setae. Labrum about twice as wide as long (Fig. 4); anterolateral margins moderately arcuately rounded. Maxillary palpus with last segment about 3 times longer than penultimate segment. Labial palpus with last segment flattened and about a fourth wider than penultimate segment (Fig. 5).

Thorax: Pronotum 0.62 mm long, 0.64 mm at widest point; posterior $\frac{4}{5}$ microreticulate (Fig. 9); crests of carinae bearing sparse, short, flattened setae; median carina uniformly wide and extending from apex almost to base (Fig. 7); lateral carinae extending from apex to base, swollen apically and gibbose slightly behind midlength; an-





Figs. 22–25. *Jolyelmis auyana,* new genus, new species: 22, male genitalia, dorsal view; 23, male genitalia, lateral view; 24, female genitalia, ventral view; Fig. 25, schematic cross section of bedrock biotope of *Jolyelmis auyana.*

terolateral angles obtuse; posterior angles acute (Fig. 7). Scutellum subtriangular; with sparse flattened setae (Fig. 15). Elytron 1.34 mm long, 0.45 mm wide; with 3 high longitudinal carinae (Fig. 8); carinae of unequal length; innermost carina shortest, extending from base about 5/9 of elytral length; middle carina longest, extending from base about 8/9 of elytral length; sublateral carina extending about 7/9 of elytral length from base at humeral angle; crests of carinae with short, flattened setae; posterior third of sutural margins subcarinate (Fig. 8); intervals with very few, fine, slender setae and moderately coarse punctures, punctures separated by 6 to 8 times puncture diameter. Prosternum in front of procoxae about as long as procoxa (Fig. 10); with a low carina extending from procoxal cavity to anterior margin of prosternum. Prosternal process broad, narrowly rimmed, converging gradually to arcuate apex (Fig. 11); with an apicomedial depression. Mesosternum with posterior margin bisinuate and deeply depressed on each side of meson (Fig. 12); with a few, fine setae. Metasternum with posteromedial 2/3 broadly, moderately deeply depressed; metasternal disc with very sparse, short, flattened setae (Fig. 13). Procoxae, mesocoxae, and metacoxae with sparse, flattened setae. Legs, except tarsi, microreticulate (Fig. 20). Tarsus with last segment swollen and as long as combined length of segments 2–4; with several long setae on ventral surface; segment 5 with additional longer, fine setae.

Abdomen: Visible sternum 1 sparsely punctate between arcuate carinae; with few, fine setae (Fig. 14); lateral surfaces with dense, slender, golden setae (Fig. 10). Sterna 2–4 sparsely microreticulate, punctate; with few, fine setae. Sternum 5 densely microreticulate. Sterna 1–3 with lateral bands of fine, golden plastron setae (Fig. 17).

Genitalia: As illustrated (Figs. 22, 23).

Female.—Externally similar to male except the posteromedial depression of the metasternum is narrower and more shallow than that on male. Genitalia as illustrated (Fig. 24).

Variations.—Six specimens of each sex were measured for length and width. Males were smaller and ranged from 1.83 to 1.96 mm in length ($\bar{X}$ = 1.85 mm) and 0.87 to 0.93 mm in width ($\bar{X}$ = 0.89 mm). Females ranged from 1.79 to 2.0 mm ($\bar{X}$ = 1.93 mm) in length and 0.87 to 0.94 mm in width ($\bar{X}$ = 0.91 mm).

Type data.—Holotype ♂: Venezuela: Bolivar: Auyantepuy, 2100 m, 10–13 Feb 1988, L. Joly, A. Chacon; deposited in the collection of the Central University of Venezuela, Maracay, Venezuela. Allotype: Same data as holotype.

Paratypes: Same data as holotype: 2 ♂, 4 ♀, deposited in the collection of the Central University of Venezuela, Maracay, Venezuela; 3 ♂, 3 ♀, deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Etymology.—Named *auyana* for the tepui from which the specimens were collected.

Habitat.—According to Joly and Chacon, specimens of this elmid species were found in cracks on an algae-covered surface of an overhanging "lip" of a cavity in a cascade (Fig. 25).

Acknowledgments

We thank L. Joly and A. Chacon for collecting the specimens, sending them for study, and sending a sketch and description of the biotope. We also thank S. G. Braden, Scanning Electron Microscopist, for taking the micrographs and P. M. Spangler for typing the manuscript.

Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 328–334

PARMOPS CORUSCANS, A NEW GENUS AND SPECIES OF FLASHLIGHT FISH (BERYCIFORMES: ANOMALOPIDAE) FROM THE SOUTH PACIFIC

Richard H. Rosenblatt and G. David Johnson

Abstract.—*Parmops coruscans,* new genus, new species, is described from a single specimen taken in 350 m at Tahiti. It is distinguished from other anomalopids by having the first four infraorbital bones expanded laterally to form a shelf beneath the eye. The light organ of *P. coruscans* is rotatable, and there is an erectile shutter. The shutter mechanism in *Parmops* is the least developed of all anomalopids.

The family Anomalopidae is a small circumtropical group of nocturnal neritic beryciform fishes. The most conspicuous defining character of the group is the presence of a luminous organ beneath the eye in which symbiotic luminous bacteria are cultured (Harvey 1922). The bacteria glow continuously, and the light organ is occluded mechanically, either by rotation of its luminous face downward or by the erection of a black elastic membrane upward over it (Johnson & Rosenblatt 1988).

The family was reviewed recently by McCosker & Rosenblatt (1987), who recognized five species in three genera and elevated the subspecies *Photoblepharon palpebratum steinitzi* to specific rank. Those authors noted the presence of two forms in the Indo-Australian area, *P. palpebratum* and *Anomalops katoptron.* Subsequently, Johnson & Rosenblatt (1988) described the mechanisms of light organ occlusion, discussed the evolution of these mechanisms in light of an hypothesized generic phylogeny, and erected a new genus, *Phthanophaneron,* for the eastern Pacific *Kryptophanaron harveyi.*

The fish collection of the Bernice P. Bishop Museum (BPBM) contains a single anomalopid specimen collected in deep water at Tahiti that cannot be assigned to any known species. Our examination of that specimen indicates that it represents a clade between *Anomalops* and *Phthanophaneron* within the phylogeny proposed by Johnson & Rosenblatt (1988, fig. 10), and thus should be placed in a new genus.

Whether the new species is restricted to deep water or, like *Kryptophanaron alfredi* and *Anomalops katoptron,* has a broad depth distribution, remains to be determined, along with all other aspects of its biology. The purpose of this paper is to describe the new species and discuss its relationships within the Anomalopidae. Methods and terminology are those of Rosenblatt & Montgomery (1976) and Johnson & Rosenblatt (1988) for external and light organ occlusion morphology, respectively.

Parmops, new genus
Figs. 1–3, Tables 1, 2

Diagnosis.—An anomalopid with the dorsolateral margins of the first four infraorbital bones expanded to form a medially sloping shelf that protrudes laterally well beyond the perimeter of the orbit, a spinous dorsal fin, two anal-fin spines, a pelvic-fin spine, a row of enlarged scutes on the belly, a fully rotatable light organ and an elastic shutter that lies flat on the floor of the orbit when relaxed.

Type species.—*Parmops coruscans,* new species.

Etymology.—From the Greek *parme,* a small shield, and *ops,* eye, in reference to the expanded infraorbitals. Gender masculine.

Parmops coruscans, new species
Figs. 1, 2, Tables 1, 2

Holotype.—BPBM 30885. A 48.2 mm SL immature individual taken 11 Aug 1985 outside the reef at Punnauia, Tahiti, Society Islands, from the stomach of a grouper, *Saloptia powelli,* caught at 350 m by "Fuller and Faty."

Description.—Counts and measurements, in mm, of the holotype: Dorsal-fin rays V—I,16; anal-fin rays II,12; pectoral-fin rays ii14i; pelvic-fin rays I,5; caudal-fin rays 10, 10+9, 10; branchiostegals 8; gill rakers 8+22; pored lateral-line scales 30; scale rows above lateral line 8; abdominal scutes 9; vertebrae 14+16. Head length 18.8; predorsal length 21.4; prepelvic length 18.6; body depth 19.1; caudal-peduncle depth 10.1; caudal-peduncle length 13.9; snout length 17.7; eye 9.0; orbit 9.4; light-organ length 6.7; light organ depth 2.6; pectoral-fin length 12.5; pelvic-fin length 9.2; first dorsal-spine length 2.9; fifth dorsal-spine length 4.4.

Body compressed, width 3.2 in depth. Back somewhat elevated, body depth 1.5 in length without head. Snout blunt, profile sloping forward without much curvature from occiput to before eye, then descending convexly to rostrum. Nostrils just before eye, anterior with thickened posterior rim. Mouth oblique, tip of lower jaw about ¼ of eye height above lower margin of eyeball, upper jaw slightly included. Maxilla extending posteriorly to about middle of eye. Posterior supramaxilla ovoid with an anterior process, covering all but posteroventral corner of maxilla. Anterior supramaxilla substantially smaller with no anteriorly directed process. Premaxillae with pronounced notch at symphysis into which lower jaw fits. Jaw teeth in bands, premaxillae with uniformly small teeth, dentaries with anterior patches of enlarged teeth that extend outside mouth. Vomer toothless, palatines with bands of teeth similar to smaller jaw teeth.

Bones of head and shoulder girdle strongly sculptured, with numerous spine-bearing ridges. Cleithrum broadly exposed, dorsal expansion with serrate posterior margin. Supracleithrum exposed, its posterior margin weakly denticulate. Infraorbitals 1–4 enlarged and laterally flared to form medially sloping shelf effectively deepening subocular pocket that accommodates light organ. Laterosensory canals of head developed as broad troughs with bony bridges. Lacrimal with three pores anteriorly followed by two larger cavities covered with smooth black membrane without papillae or pores. Postorbital canal with two bony bridges delineating three membrane-roofed spaces. Preopercular canal with two bony bridges near angle. Mandibular canal with two pores through bone anteriorly, followed posteriorly by long trough with two bony bridges near junction with preopercular canal. Canals of cranium covered by skin that appears smooth and entire, except for two lateral and one medial frontal pores above orbit, two small pores on supraorbital canal, and small temporal pore on right side. Eye prominent, its diameter about equal to postorbital head length. Much of cornea black, with subspherical clear window 6.0 mm long by 5.0 mm high. Pupil 4.0 mm in diameter. Single fleshy tubercle on posterior margin of eye on level with lower margin of pupil. Ovoid luminous organ below eye, free except at anterior end, rotatable so that luminous face can be rotated downward into pocket formed by flared infraorbitals. Outer margin of adpressed organ well below infraorbital rim. Black elastic shutter membrane attached along lateral margin of suborbital pocket, lying flat on floor of pocket when relaxed, with free margin directed medially.

Scales strongly ctenoid (ct′ of Johnson

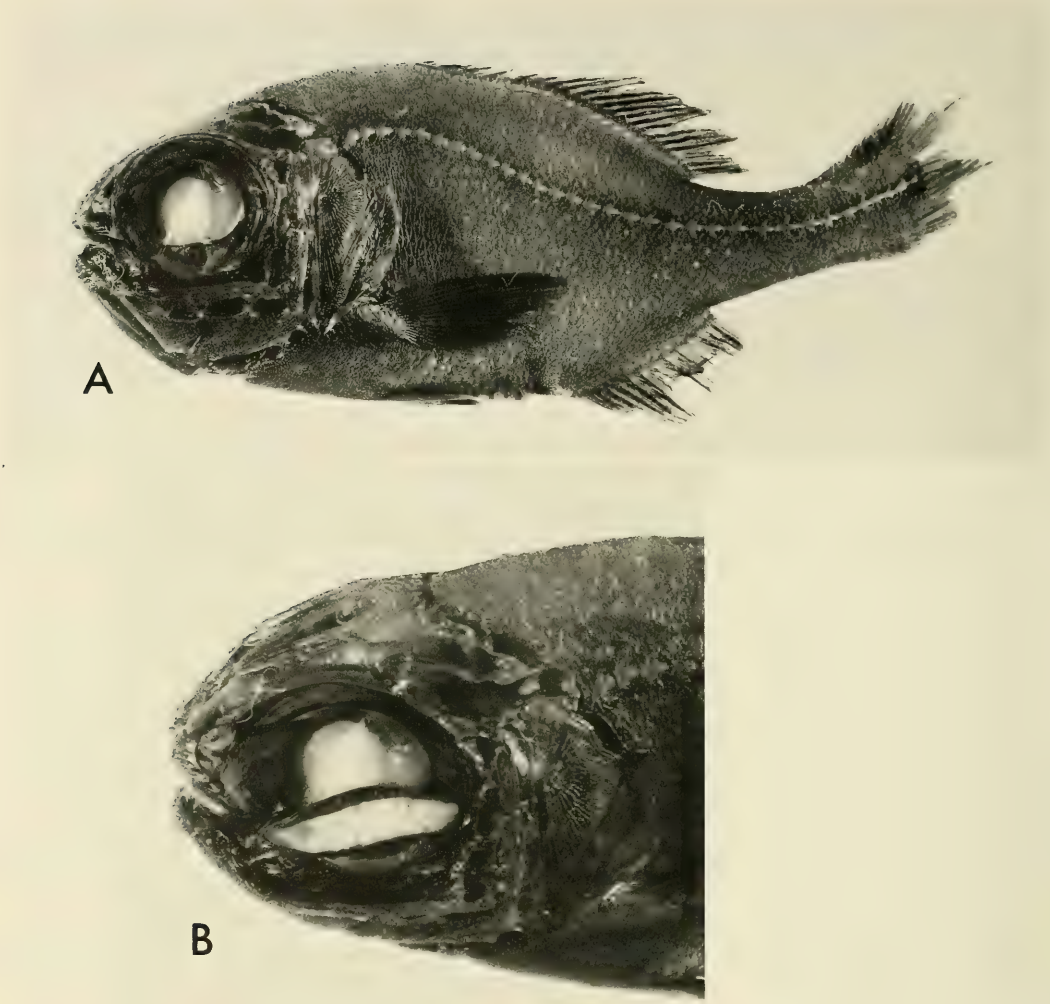


Fig. 1. Holotype of *Parmops coruscans,* BPBM 30885. A. Whole specimen in lateral view, light organ occluded. B. Head in dorsolateral view, light organ exposed.

1984), small, and difficult to enumerate because of irregular arrangement, approximately 100 lateral body rows. Head scaleless except for a few irregular scales at anterodorsal corner of opercle, along preopercle and on cheek. Gular isthmus naked, with transverse fleshy ridges. No cycloid scales on body. Scale sheaths well-developed at bases of dorsal and anal fins. Midventral row of 9 enlarged keeled scales (scutes) along abdomen.

Gill rakers on first arch well developed, lath-like; length of first raker below angle about ½ eye diameter; rakers becoming shorter on succeeding arches, those on last arch nubbins. Pseudobranch well developed, with about 18 filaments, longest slightly longer than filaments of first gill arch.

Spinous dorsal fin relatively low, first spine about half length of succeeding four, which are subequal. Dorsal and anal soft rays mostly broken. First anal spine about

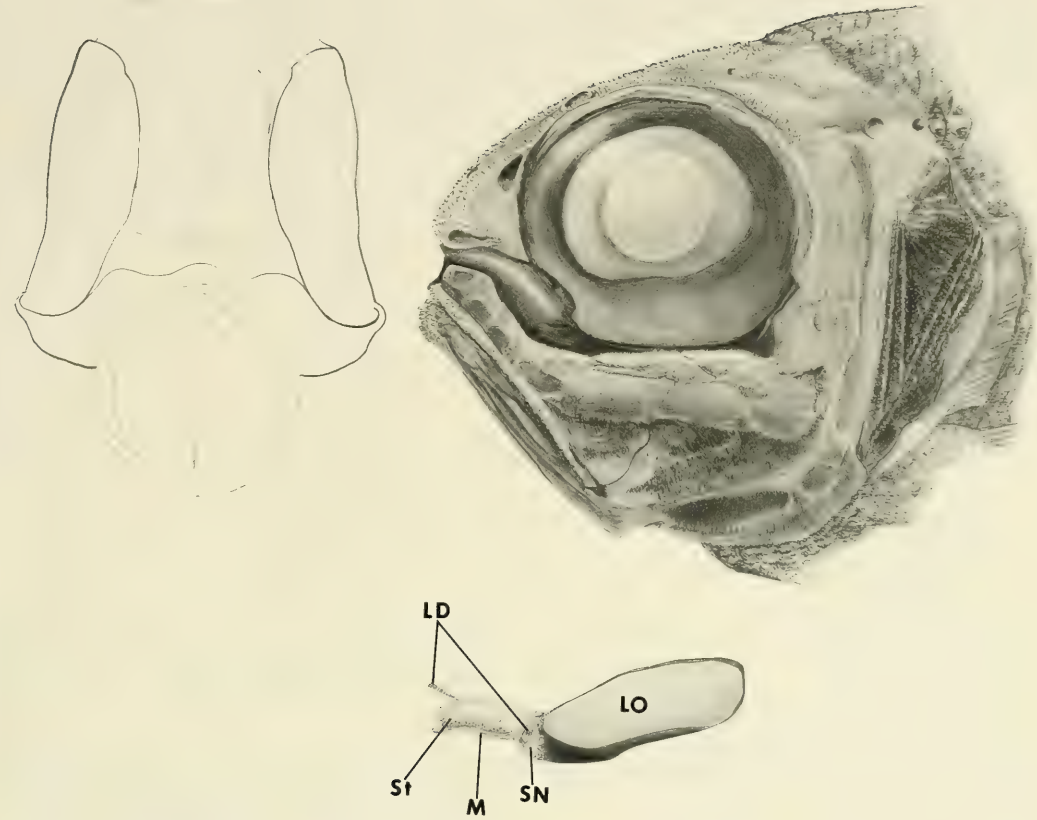


Fig. 2. Holotype of *Parmops coruscans*. Head, light organ occluded, with outline of frontal view to left and light organ and associated structures, removed, below: LD, Ligament of Diogenes; LO, light organ; M, stalk muscle; SN, rudiment of shutter knob; ST, stalk.

equal in length to first dorsal spine. Second anal-fin ray a spine in transition, segmented at tip. Caudal-fin rays broken.

Pectoral fin angulate, length about 1.5 in head, third through sixth rays subequal and longest. Pelvic fin shorter than pectoral, extending to within 0.4 eye diameter of anal-fin origin. Color black, fins and lower part of head darkest. Lateral line conspicuously paler than rest of body.

Etymology.—From the Latin *coruscans,* sparkling, in reference to the subocular light organ.

Occlusion mechanism.—The light organ, stalk and supporting cup are shown in Fig. 2. The light organ is borne on a fibrocartilage stalk that is continuous across the snout with no attenuation at the commissure. Posteriorly the stalk articulates loosely with the supporting fibrocartilage cup of the organ and is attached to it by two short ligaments. The anteroventral corner of the cup extends forward as a short process that is connected directly by one of the short ligaments to the posteroventral corner of the stalk, which bears no ventral hook. There is no discrete shutter knob, but there is a slight thickening at the anterodorsal corner of the shutter. The cup is a crescentic structure that embraces the anterior end of the light organ and extends posteriorly along about two-thirds of its ventral surface. Anteriorly, the cup is expanded as a medially projecting shelf. The stalk muscle is relatively small,

Table 1.—States of characters not associated with light-organ complex in *Parmops*. (Characters numbered as in Johnson & Rosenblatt 1988).

1	Epipleural ribs	2
2	Branchiostegals	Spiny
3	Openings in pars jugularis	?
4	Parasphenoid flanges	?
5	Swimbladder stay	—
6	Postorbital papillae	1
7	Cephalic sensory canal covering	Smooth**
8	Lateral-line tubes	Closed
9	Midventral scutes	Continuous
10	Dorsal Fin / Predorsals	V—I, 16 / 0/0/1+1/
11	Supramaxillae	2*
12	Transverse ridges on gular isthmus	+*
13	Lateral dentary tooth patch	Large "V"*
14	Body scale rows	ca. 100*
15	Reflective or transparent lateral line scales	+*
16	Pelvic spine	+
17	Anal spines	II
18	Vertebrae	14+16
19	Corner of maxilla	Smooth

* Derived states shared with *Phthanophaneron* (lacks 15), *Kryptophanaron,* and *Photoblepharon.*

** Derived state shared as a homoplasy with *Kryptophanaron.*

Table 2.—Light-organ associated character states in *Parmops*. (Characters numbered as in Johnson & Rosenblatt 1988).

I	Attachment of LD on cup	Lateral
II	Attachment of LD anteriorly	Maxilla
III	Cup with medial shelf	Moderate
IV	Insertion of stalk muscle dorsally	Ligament to cup
V	Stalk with inward flexure at cup articulation	—
VI	Rotation pad	—
VII	Postocular skin flap	—
VIIIa	Erectile shutter	+*
VIIIb	Shutter knob	—
IX	Stalk hook	—
X	Stalk continuous across snout	+*
XIa	EM with groove	+*
XIb	EM with medial swelling	—
XII	Hook and shutter knob intimately associated	NA
XIII	Cup process attached to stalk hook by ligament	NA
XIV	Organ rotatable	+

* Derived states, all shared with *Phthanophaneron, Kryptophanaron,* and *Photoblepharon.*

with little differentiation between the dorsal portion, which inserts on the dorsal ligament that connects the cup and stalk, and the ventral portion, which inserts on the articular termination of the stalk. The Ligament of Diogenes attaches to the anteromedial corner of the cup shelf and runs anterodorsally, passes over a slight groove in the ethmomaxillary ligament at its forward flexure, and inserts on the lateral face of the rostral cartilage. The ethmomaxillary ligament originates dorsally on the mesethmoid and extends ventrally, flexes anteroventrally at the groove, and then passes around the cartilaginous tip of the palatine to insert on the ventrolateral margin of the maxilla just ventral to its head. The groove in the ethmomaxillary ligament is weakly developed and there is no notable swelling on the medial surface of the latter. The ethmomaxillary ligament branches just dorsal to its insertion on the maxilla, giving rise to a broader but thinner segment that passes ventrally to insert on the palatine.

Relationships.—In physiognomy, *Parmops* most closely resembles *Phthanophaneron,* and this similarity is reflected in the primitive nature of the light occlusion mechanism as well. Table 1 lists characters not associated with the light organ mechanism and Table 2 lists those that are. Our hypothesis of relationships based on these characters is presented in Fig. 3. Among the characters not associated with the light organ mechanism, *Parmops* shares five derived states with the *Phthanophaneron-Kryptophanaron-Photoblepharon* (hereafter *P.-K.-P.*) clade and none with *Anomalops.* For one of those five apomorphies, the presence of reflective or transparent lateral-line scales (character 15), there is an alternative interpretation equally parsimonious to the topology shown on the cladogram, i.e., independent acquisition in *Parmops* and at the *K.-P.* node rather than reversal in

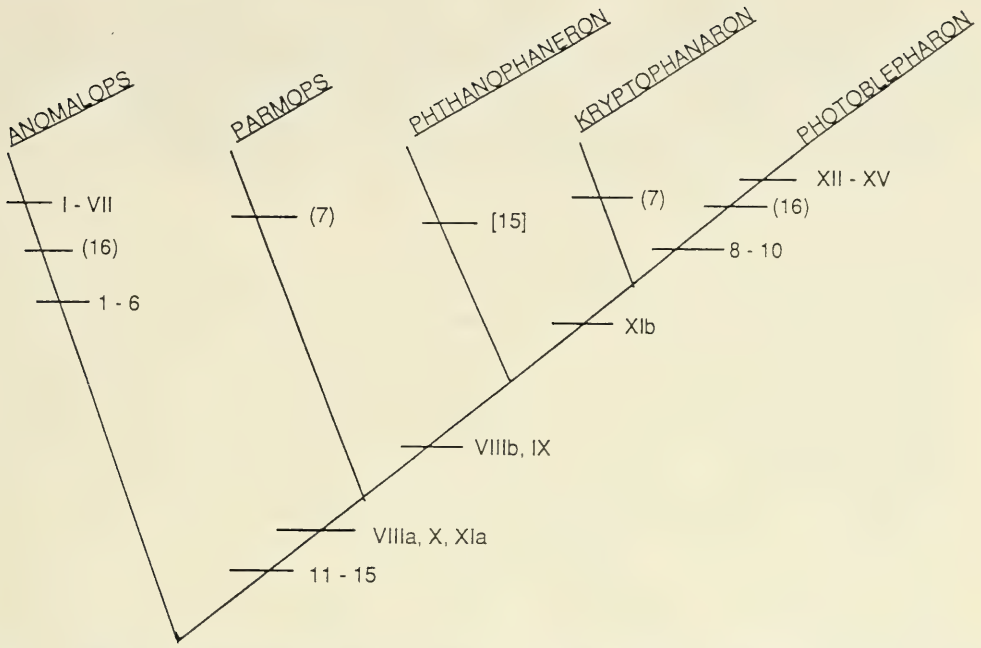


Fig. 3. Cladogram of anomalopid genera. Characters as in Tables 1 and 2. Parentheses and brackets respectively denote hypothesized independent acquisitions and reversals.

Phthanophaneron. Of the light-organ associated characters, *Parmops* shares three, an erectile shutter, a continuous stalk, and a groove in the ethmomaxillary ligament, with the *P.-K.-P.* clade. *Parmops* is primitive with respect to members of that clade in two states, absence of a stalk hook and shutter knob. *Parmops* is thus placed at the base of the shutter-mechanism lineage, as the sister group of the *P.-K.-P.* clade. These four genera ostensively provide a rare illustration of the gradual evolutionary elaboration of a functional complex, in which each genus exhibits a slightly more intricate and integrated linkage system to effect shutter erection.

Acknowledgments

We wish to thank J. E. McCosker for serendipitously bringing the present specimen to our attention. L. Wrobel obtained the specimen, recognized its interest, and preserved it. J. E. Randall, Bernice P. Bishop Museum, made it available to us for study. W. D. Anderson, R. Birdsong, J. E. McCosker and R. Vari critically read the manuscript. The drawings were executed by P. Hollingsworth.

Literature Cited

Harvey, E. N. 1922. The production of light by the fishes, *Photoblepharon* and *Anomalops*.—Publications of the Carnegie Institution, Washington 312:45–61.

Johnson, G. D. 1984. Percoidei: development and relationships. Pp. 464–498 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds., Ontogeny and systematics of fishes. American Society of Ichthyologists and Herpetologists Special Publication No. 1.

———, & R. H. Rosenblatt. 1988. Mechanisms of light organ occlusion in flashlight fishes, family Anomalopidae (Teleostei: Beryciformes), and the evolution of the group.—Zoological Journal of the Linnean Society 94:65–96.

McCosker, J. E., & R. H. Rosenblatt. 1987. Notes on the biology, taxonomy, and distribution of

anomalopid fishes (Anomalopidae: Beryciformes).—Japanese Journal of Ichthyology 34: 157–164.

Rosenblatt, R. H., & W. L. Montgomery. 1976. *Kryptophaneron harveyi,* a new anomalopid fish from the eastern tropical Pacific, and the evolution of the Anomalopidae.—Copeia 1976:510–515.

(RHR) Scripps Institution of Oceanography, La Jolla, California 92093; (GDJ) Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 335–343

A NEW SPECIES OF THE ANTHIINE GENUS *PLECTRANTHIAS* (PISCES: SERRANIDAE) FROM THE SALA Y GÓMEZ RIDGE IN THE EASTERN SOUTH PACIFIC, WITH COMMENTS ON *P. EXSUL*

William D. Anderson, Jr. and John E. Randall

Abstract.—*Plectranthias parini,* a new species of anthiine serranid fish, is described from a single specimen collected from the Sala y Gómez Ridge in the eastern South Pacific, about 2700 km west of Chile at 25°02.6′S. It is distinguished from all other species of *Plectranthias* by the following combination of characters: scales with marginal cteni and ctenial bases, vertebrae 26 (10 precaudal + 16 caudal), predorsal bones 3, principal caudal-fin rays 17 (9 + 8), pectoral-fin rays 16, gillrakers 26 (8 + 18), and tubed lateral-line scales 37 left (40 right), and by the presence of two orange-red bars on the posterior half of the body, one just anterior to the anal fin and the other terminating ventrally posterior to the anal fin. This new species is the second species of *Plectranthias* to be reported from the eastern Pacific. It is briefly compared with other species of the genus. In addition new material of *P. exsul,* the only other eastern Pacific *Plectranthias* known, is discussed.

N. V. Parin sent the junior author a specimen of an undescribed species of anthiine serranid fish that was collected over the Sala y Gómez Ridge in the eastern South Pacific by personnel aboard a Soviet research vessel. Johnson (1983) provided strong evidence that the Serranidae are a monophyletic assemblage, but he did not delimit the Anthiinae, and this subfamily remains inadequately circumscribed—despite the facts that Roberts (1989) characterized it and Anderson et al. (1990) provided a preliminary definition of it. We assign the new species, described herein, to *Plectranthias* on the basis of its close resemblance to a number of species currently relegated to that genus. Randall (1980) revised (but did not demonstrate the monophyly of) *Plectranthias* Bleeker, 1873, subsuming eight other genera into its synonymy while recognizing 17 previously described species and 13 new ones as valid members of the genus. Since Randall's revision, seven other species of *Plectranthias* have been described as new: *P. randalli* Fourmanoir & Rivaton, 1980; *P. altipinnatus* Katayama & Masuda, 1980; *P. maculatus* Fourmanoir, 1982; *P. barroi* Fourmanoir, 1982; *P. fijiensis* Raj & Seeto, 1983; *P. exsul* Heemstra & Anderson, 1983; and *P. bilaticlavia* Paulin & Roberts, 1987. There are several other undescribed species of *Plectranthias* (in addition to the one described herein) in museum collections. The objectives of this paper are to describe the new species, to compare it with other species of the genus, and to discuss new material of *P. exsul.*

Institutional abbreviations are as listed in Leviton et al. (1985). Methods for making counts and measurements are those of Anderson et al. (1990). Most measurements are presented as percentages of the standard length (SL), but some are given as quotients of SL, head length, orbital diameter, or snout

length; these quotients are rounded to the nearest 0.05. Osteological data are from radiographs.

Plectranthias parini, new species
Figs. 1, 2A, Tables 1, 2

Holotype.—USNM 312925, 84.7 mm SL; 25°02.6'S, 97°29.2'W; 260–272 m; R/V *Prof. Shtokman* cruise 18, station 1984; 3–4 May 1987; bottom otter trawl.

Diagnosis.—A species of *Plectranthias* distinguishable from all other species of Serranidae by the following combination of characters. Dorsal-fin rays X, 16; second soft ray of dorsal fin produced. Anal-fin rays III, 7. Pectoral-fin rays 16. Posterior margin of caudal fin truncate except two dorsalmost branched rays produced; principal rays 9 + 8; branched rays 8 + 7. Vertebrae 26 (10 precaudal + 16 caudal). Formula for configuration of predorsal (supraneural) bones, anterior neural spines, and anterior dorsal pterygiophores 0/0+0/2/1+1/1/ (using symbolization of Ahlstrom et al. 1976). Tubed lateral-line scales 37 (left), 40 (right). Gillrakers, including rudiments, on first gill arch 8 + 18—total 26 (both sides). Preopercle without antrorse spines, both free margins serrate. Posterior margin of bony opercle with three spinous processes, middle one best developed, but ventralmost well developed. Interopercle and subopercle serrate near their junction. Interorbital region flattened. Scales ctenoid, resembling those of serranine serranids (i.e, with rows of ctenial bases [Hughes 1981] present proximal to marginal cteni). No scales on lateral aspect of snout, maxilla, anterior three-fourths of lower jaw, gular region, branchiostegals, or branchiostegal membranes. Two broad orange-red bars on posterior half of body, one just anterior to anal fin, the other terminating ventrally posterior to anal fin.

Description.—Characters presented in the diagnosis are not repeated unless necessary for clarification. Most morphometric data appear in Table 1. Mouth nearly terminal, lower jaw exceeding upper jaw very slightly. Premaxillae protrusile. Posterodorsal border of maxilla not covered by elements of circumorbital series when mouth closed. Maxilla reaching vertical through posterior border of eye. Maxilla not abruptly widened distally, without a hook or shelf on labial border. Posteroventral corner of maxilla with a poorly developed rounded extension. Small splint-like supramaxilla present. Nares rather close together; anterior naris in a tube which is short anteriorly and well developed laterally, medially, and posteriorly; posterior part of tube not reaching posterior naris when reflected; posterior naris dorsoventrally elliptical and larger than anterior naris. Orbital margin without fleshy papillae. Serrae on preopercle 43 left (ca. 43 right), on interopercle 4 left (ca. 4 right), on subopercle 8 left (10 right). Branchiostegals 7. Longest gillrakers longer than longest gill filaments. Pseudobranch with 25 filaments. Dorsal fin single, not incised between spinous and soft portions. Second soft ray of anal fin slightly produced. Second anal spine more robust than first or third, almost twice as long as first, slightly longer than third. Pectoral fin symmetrical, middle rays longest; dorsalmost and ventralmost rays unbranched, other rays branched; pectoral fin reaching vertical through base of fourth dorsal soft ray and base of third anal soft ray. Pelvic-fin rays I, 5; pelvic fin inserted beneath base of pectoral fin, the tip reaching a vertical through base of first dorsal soft ray, falling short of origin of anal fin. Procurrent caudal-fin rays 8 dorsally, 7 ventrally. Pleural ribs on vertebrae 3 through 10. Epipleural ribs associated with first 10 vertebrae. Epihaemal ribs (bones in the same series as the epipleural ribs which appear to be modified intermuscular bones; see Stiassny & Jensen 1987:300) on vertebrae 11 through 13. Posteriormost complete pterygiophore of anal fin trisegmental; no trisegmental pterygiophores associated with dorsal fin. Procurrent spur (Johnson 1975) absent; penultimate ventral procurrent caudal-fin ray not shortened basally. Parhypural with well-developed hypurapophysis.

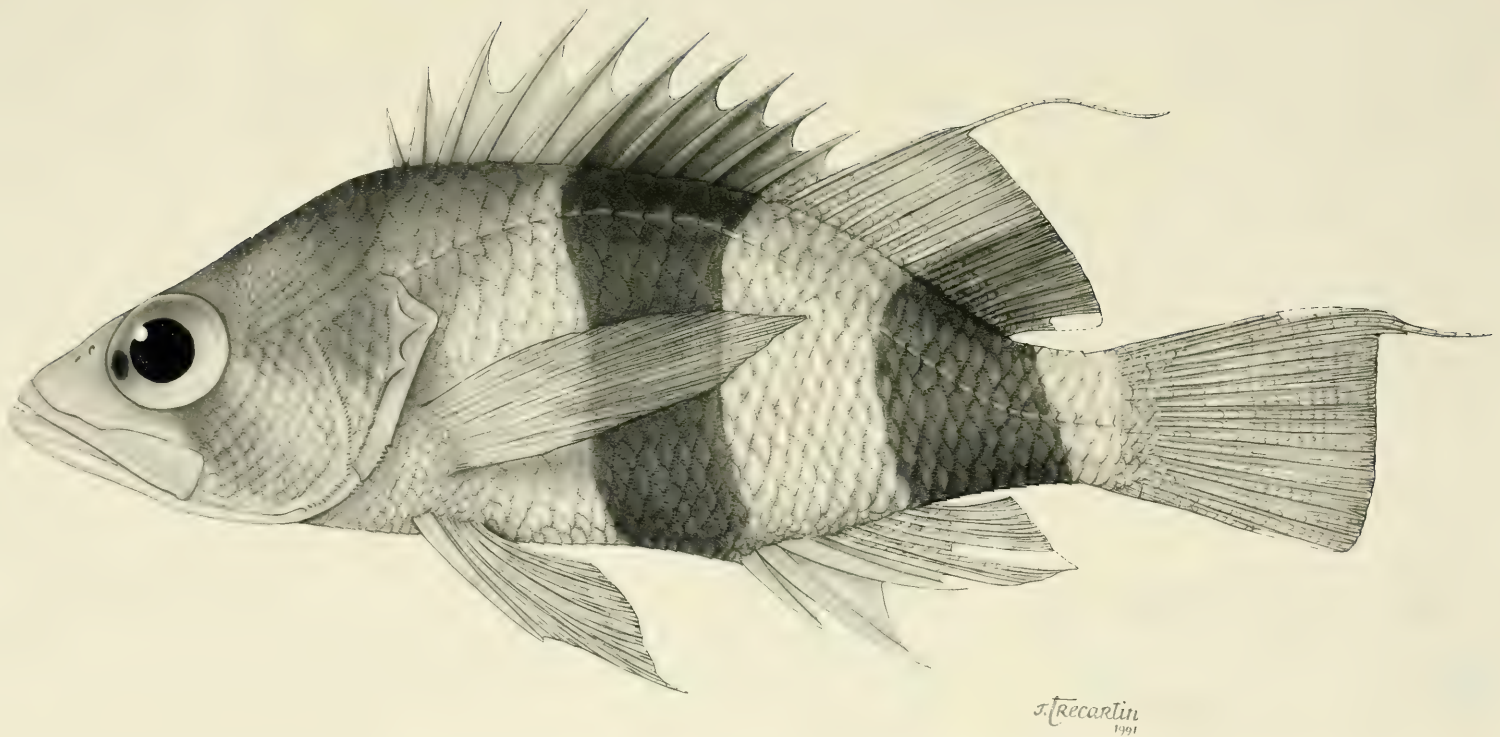


Fig. 1. Holotype of *Plectranthias parini,* USNM 312925, 84.7 mm SL; Sala y Gómez Ridge, eastern South Pacific; pattern of coloration drawn from color transparency. (Posterior bar does not extend as far out on dorsal fin as shown. See Fig. 2A for more accurate representation.

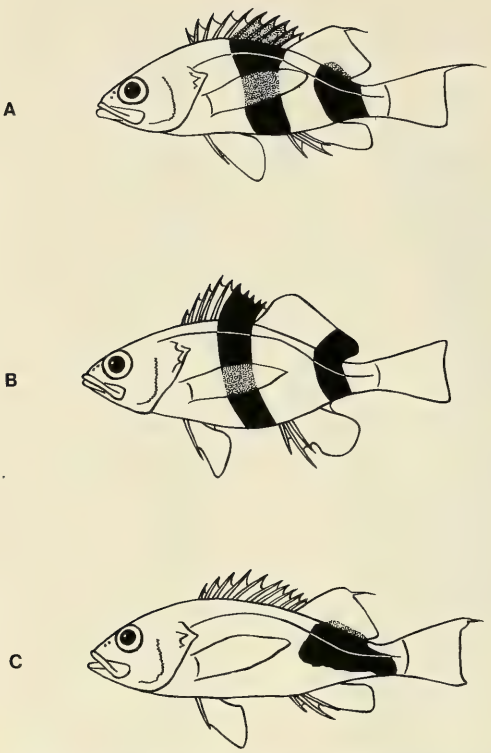


Fig. 2. Drawings of specimens of three species of *Plectranthias* to show patterns of coloration. (A) Holotype of *P. parini,* USNM 312925, 84.7 mm SL, from color transparency; (B) paratype of *P. bilaticlavia,* NMNZ P.20264, 70.9 mm SL, from Paulin & Roberts, 1987 (redrawn with permission); (C) *P. exsul,* from color transparency.

Autogenous hypurals 5. Epurals 3. Uroneurals 1 pair (posterior pair absent). Lateral line complete, running parallel to dorsal body contour below dorsal fin, curving to near mid-lateral axis of body on caudal peduncle. Tubes in lateral-line scales branched anteriorly, simple posteriorly. No secondary squamation. Most of head covered with scales; most of dorsum of snout, lateral aspect of snout, maxilla, supramaxilla, lachrymal, almost all of suborbital region, most of lower jaw, gular region, branchiostegals, and branchiostegal membranes without scales. Interorbital region heavily covered with scales; posterior one-fourth of lower jaw with some scales. Posterior part of spinous dorsal fin scaly basally; soft dorsal and anal scaly for one-third to one-half distances from bases to distal margins of fins; pectoral, pelvic, and caudal fins scaly basally; pelvic axillary process poorly developed; short scaly interpelvic process between bases of pelvic fins. Rows of cheek scales 9 (both sides). Scale rows between lateral-line and mid-base of spinous dorsal fin 2 (both sides). Scales from dorsal-fin origin to lateral line 3 (both sides). Scales from anal-fin origin to lateral line ca. 15 left, ca. 16 right. Circumpeduncular scales 17.

Premaxilla with a band of small conical teeth, band broadest at anterior end of jaw near symphysial diastema where innermost teeth variously enlarged into much bigger conical and caniniform teeth; a robust canine near anterior end of jaw. Dentary with a row of small conical teeth extending from near posterior end of bone to about mid-length of jaw; three well-developed canines at about mid-length of jaw on left (one on right); anterior to canines a band of small conical teeth extending to symphysial diastema; band expanded at anterior end of jaw where innermost teeth variously enlarged into much bigger conical and caniniform teeth; exserted canine at anterior end of jaw. Vomer and palatine with conical teeth. Vomerine teeth in chevron-shaped patch, without backward prolongation. Palatine, for most of its length, with teeth in a narrow band; anteriorly band of teeth wider. No teeth on tongue or pterygoids.

Body length (at dorsal-fin origin) 2.80, head length 2.55 in SL. Bony orbital diameter 3.30 in head length. Bony interorbital width 8.15 in head length, 2.45 in bony orbital diameter. Snout length 1.45 in bony orbital diameter. Internarial distance 6.90 in snout length.

Coloration.—Color from a transparency taken shortly after capture of the holotype: Head mainly pale orange, dull yellow ventrally. Iris dull yellow except for a hint of reddish coloration on posterior border. Body with an overall orange cast dorsally, yellowish ventrally. Two orange-red parallel bars

Table 1.—Morphometric data for the holotype of *Plectranthias parini* and specimens of *P. exsul* and *P. bilaticlavia*. Data on *P. bilaticlavia*, with the exception of internarial distance, are from Paulin & Roberts 1987. Standard lengths are in mm; other measurements, in percentages of standard length; > = slightly damaged.

Character	*P. parini*	*P. exsul*		*P. bilaticlavia*	
		n	Range	*n*	Range
Standard length	84.7	9	37.6–158	3	36.5–70.9
Head, length	39.4	9	37.0–39.1	3	39.4–41.1
Snout, length	8.1	9	8.0–10.6	3	7.9–10.2
Orbit, diameter	11.9	9	8.4–11.2	3	12.3–15.4
Postorbital length of head	19.4	9	17.2–20.0		
Upper jaw, length	18.9	9	16.0–19.6	3	17.2–18.8
Maxilla, width	5.0	9	4.8–6.3		
Interorbital width	4.8	9	5.1–6.5	3	4.2–5.4
Internarial distance	1.2	2	0.8–1.1	2	0.7–1.1
Body, depth	35.8	9	30.1–39.6	3	32.9–35.3
Body, width	17.8	4	17.5–18.6	3	16.1–18.3
Predorsal length	40.4	9	35.8–39.9	3	39.9–41.8
Prepelvic length	37.7	2	36.5–40.4	3	29.5–46.5
Preanal length	68.5	9	64.1–70.6	3	69.5–72.0
Caudal peduncle, length	19.7	9	18.6–22.7		
Caudal peduncle, depth	11.7	9	9.8–13.1	3	10.0–12.8
Dorsal-fin base, length	56.1	2	52.6–52.8	3	46.3–53.4
Pectoral fin, length	36.7	9	ca. 30.1–34.3	3	30.4–33.7
Pelvic fin, length	28.9	8	ca. 22.3–26.1	3	25.2–27.6
Anal-fin base, length	16.8	2	16.6–16.8	3	16.7–19.1
Anal fin, length	33.8	8	26.5–ca. 30.8		
Upper caudal-fin lobe, length	ca. 35.5	8	>24.4–>30.4		
Lower caudal-fin lobe, length	26.6	8	22.2–>27.4		
First dorsal spine, length	5.8	6	6.2–>7.9	3	6.8–7.1
Third dorsal spine, length	13.7	9	14.3–>16.8		
Fourth dorsal spine, length	17.9	9	>14.1–>18.8		
Tenth dorsal spine, length	12.0	8	9.1–11.3		
Longest dorsal spine, length	18.3 (5th)	9	16.3–19.9 (4th or 5th)	3	15.8–19.4
Longest dorsal soft ray, length	ca. 34.5 (2nd)	8	ca. 16.2–>25.5 (2nd)	2	13.6–22.2
First anal spine, length	10.5	9	7.6–11.3	3	10.1–12.1
Second anal spine, length	19.2	8	16.0–20.7	3	17.8–22.0
Third anal spine, length	17.9	9	14.7–15.9	3	14.5–15.4
Longest anal soft ray, length	25.4 (2nd)	1	ca. 21.6 (3rd)	3	19.7–25.6
Pelvic spine, length	17.8	4	14.2–16.9	3	16.7–19.6

Table 2.—Frequency distributions of numbers of tubed lateral-line scales in three species of *Plectranthias*. Counts of scales were made from both sides of most specimens; *n* = number of specimens examined.

Species	*n*	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	$\bar{X}$
P. exsul																	
Juan Fernández	5										1	2	1	4	1	1	43.50
Nazca Ridge	5					1	—	—	2	4	1	1					39.67
P. parini	1						1	—	—	1							38.50
P. bilaticlavia	2	1	2														32.67

Table 3.—Morphometric data on specimens of *Plectranthias exsul* from the Juan Fernández Islands and the Nazca Ridge. Standard lengths are in mm; other measurements in percentages of standard length.

Measurement	Juan Fernández Islands			Nazca Ridge		
	n	Range	$\bar{X}$	*n*	Range	$\bar{X}$
Standard length	5	134–158	149	4	115–150	130
Postorbital length of head	5	18.3–20.0	19.02	4	17.2–19.0	18.32
Upper jaw, length	5	18.3–19.6	19.04	4	17.5–18.7	18.15
Maxilla, width	5	5.5–6.3	5.90	4	5.0–5.6	5.32
Body, depth	5	35.2–39.6	37.06	4	33.4–36.1	34.35
Preanal length	5	64.7–69.3	66.30	4	65.8–70.6	69.08
Caudal peduncle, depth	5	10.7–13.1	11.76	4	10.3–10.9	10.70
Longest dorsal spine length	5	18.1–19.9	18.76	3	16.3–18.2	17.53

on body; first originating well out on interradial membranes 5 through 9 of spinous portion of dorsal fin and extending slightly obliquely to terminate ventrally almost entirely anterior to first anal spine—first bar slightly broader at dorsal-fin base than at ventral termination; second bar beginning on bases of posterior dorsal soft rays and on dorsum of anterior part of caudal peduncle and extending slightly obliquely to terminate ventrally posterior to anal-fin base; bars, particularly posterior one, somewhat wider than comparable bars in *Plectranthias bilaticlavia* (compare Figs. 2A & B). Except where orange-red bars encroach on dorsal fin, fins mostly pallid, but anteriormost interradial membranes of spinous dorsal fin with some yellow-orange. In alcohol, pigmentation lost except remnants of vertical bars still evident.

Comparisons.—*Plectranthias parini,* with 37 to 40 lateral-line scales, has more lateral-line scales than any other species in the genus except *P. kelloggi* (Jordan & Evermann, 1903)—32 to 38, *P. taylori* Randall, 1980—40 or 41, *P. randalli* Fourmanoir & Rivaton, 1980—39, and *P. exsul* Heemstra & Anderson, 1983—36 to 46. Three other species of *Plectranthias* have counts of lateral-line scales closely approaching those of *P. parini*—*P. alleni* Randall, 1980, and *P. kamii* Randall, 1980, each with 33 to 36, and *P. barroi* Fourmanoir, 1982, with 35 or 36. *Plectranthias parini,* with a total of 26 gillrakers on the first gill arch, can be distinguished from six of the seven above species by counts of the total number of gillrakers on the first gill arch: *P. taylori, P. randalli, P. alleni,* and *P. kamii* (each with 20 or fewer), *P. kelloggi* (with 20 to 24), and *P. barroi* (with 31 to 35).

Plectranthias parini (from the Sala y Gómez Ridge) is apparently closely related to *P. exsul* (from the Juan Fernández Islands and the Nazca Ridge in the eastern South Pacific). In addition to having similar counts of lateral-line scales, there is a slight overlap in total number of gillrakers on the first arch—26 in *P. parini,* 26 to 31 (7 of 10 specimens with 28 or 29) in *P. exsul.* The two species have distinctly different patterns of coloration (see descriptions of live coloration and Figs. 2A & C). In *P. parini* the longest dorsal soft ray is appreciably longer that in *P. exsul* (Table 1). Also, measurements of a number of other body parts of *P. parini* fall beyond the ranges of those for *P. exsul*; this is particularly noticeable for the pectoral, pelvic, and anal fins, the upper caudal-fin lobe, and the third anal spine (Table 1).

Not only does *P. kelloggi* (known from off Japan, New Caledonia, and Hawaii) have a slightly lower gillraker count than does *P. parini,* it also has a color pattern reminiscent of that of *P. exsul* (compare Randall, 1980:146, fig. 15, and Fig. 2C) and distinctly different from that of *P. parini* (compare Randall, 1980:146, fig. 15, and Fig. 2A).

Plectranthias parini displays a pattern of

coloration very much like that of *P. bilaticlavia* Paulin & Roberts, 1987, (known only from off the Kermadec Islands off northern New Zealand) (compare Figs. 2A & B), but it is separated easily from *P. bilaticlavia* in having more lateral-line scales (37 to 40 vs. 32 or 33, Table 2) and more dorsal soft rays (16 vs. 15). In *P. parini* the longest dorsal soft ray is much longer than in *P. bilaticlavia,* and the measurements of a number of other body parts (most noticeably the pectoral fin, dorsal-fin base, and third anal spine) fall outside the ranges for those of *P. bilaticlavia* (Table 1). Paulin & Roberts (1987) reported that one of the three known specimens of *P. bilaticlavia* (the holotype) has 27 vertebrae (10 precaudal + 17 caudal); the other two have 26 (10 + 16). (We have examined radiographs of the holotype and one of the paratypes of *P. bilaticlavia* and confirm the counts reported in the literature.) *Plectranthias parini* has 26 (10 + 16).

Distribution.—*Plectranthias parini* is known only from the type locality on the Sala y Gómez Ridge in the eastern South Pacific, about 2700 km west of Chile. The type locality is approximately 1200 km to the west of the nearest locality of capture of the related species *P. exsul.*

Etymology.—We take pleasure in naming this new species for N. V. Parin who provided the holotype and a color transparency of it.

Plectranthias exsul
Heemstra & Anderson, 1983
Fig. 2C, Tables 1–3

Since the publication of the original description of *Plectranthias exsul* (from off the Juan Fernández Islands and the Nazca Ridge in the eastern South Pacific) by Heemstra and Anderson (1983), three additional specimens from the Nazca Ridge have become available; all three are smaller (37.6, 115, 122 mm SL) than any of the specimens (133–158 mm SL) previously studied. In addition, C. D. Roberts brought to our attention another specimen (154 mm SL) of *P. exsul* from off the Juan Fernández Islands. The new material agrees reasonably well with the specimens in the original description with the exceptions of counts of tubed lateral-line scales in specimens from the Nazca Ridge. The counts for lateral-line scales provided by Heemstra & Anderson (1983) range from 40 to 46, but those for the additional Nazca Ridge specimens range from 36 to 40. The range of numbers of lateral-line scales for the five specimens from the Juan Fernández Islands is 41 to 46 ($\bar{X}$ = 43.50, based on counts from both sides of each specimen; Table 2) and that for the five specimens from the Nazca Ridge is 36 to 42 ($\bar{X}$ = 39.67, based on nine counts; Table 2). Discrepancies in the ranges of measurements of certain body parts of specimens from the two localities may be indicative of real differences between the populations (Table 3), but it is possible also that these differences are artifacts of the small sample sizes.

At the time of publication of the original description of *P. exsul* no information was available on live coloration. A color transparency taken shortly after capture of a specimen of this species reveals: Head dark red-orange dorsally, with somewhat diffuse brighter red-orange area on preopercle near orbit; posterior and ventral parts of head lighter—mostly dull yellow. Iris dull yellow anteriorly and posteriorly, the yellow bordered by a narrow red-orange rim anteriorly, suffused with red-orange posteriorly; dorsal and ventral portions of iris largely melanistic. Body generally with reddish-orange cast, darker dorsally; a well-defined brilliant red oblong area extending from bases of posterior dorsal soft rays ventrally to just below midline and then posteriorly over middle of caudal peduncle to reach mid-ventral line near base of caudal fin (see pattern of coloration in Fig. 2C). Fins with dull yellowish cast (some dull orange on spinous portion of dorsal fin), but without any distinctive pigmentation.

In order to distinguish *P. exsul* from other species of *Plectranthias,* see section on comparisons under *P. parini* and Heemstra & Anderson (1983).

Other Material Examined

Plectranthias exsul.—Nazca Ridge: BPBM 29400 (one specimen, 37.6 mm SL); 25°37′S, 85°26′W; 190 m; 4 Oct 1980; R/V *Ikhtiandr*; trawl. USNM 312926 (1, 115); 25°43′S, 85°22′W; 185 to 200 m; 5 Sep 1983; R/V Prof. *Mesyatzev*; bottom trawl. USNM 312927 (1, 122); 25°41.7′S, 85°23.7′W; 162 to 168 m; 26 Apr 1987; R/V *Prof. Shtokman*; bottom trawl. Juan Fernández: MNHNC P.5611 (1, 154); 33°37′15″S, 78°49′56″W; Jan–Feb 1970.

Plectranthias bilaticlavia.—Kermadec Islands: Holotype: NMNZ P.14024 (36.5 mm SL); Raoul Island, off Bell's Flat; 164 to 210 m; 4 Apr 1973; R/V *Acheron*; Agassiz trawl. Paratype: NMNZ P.20264 (70.9 mm SL); south of L'Esperance Rock; 270 m; 18 Jul 1974; Agassiz trawl.

Acknowledgments

N. V. Parin gave us the opportunity to describe the new species, provided us with color transparencies of both the new species and *Plectranthias exsul,* sent us new material of *P. exsul,* and allowed us to deposit specimens in the Division of Fishes, USNM; C. D. Paulin permitted us to examine the specimens of *P. bilaticlavia*; C. D. Roberts made us aware of a specimen of *P. exsul* and furnished a radiograph of the holotype of *P. bilaticlavia*; C. D. Paulin, C. D. Roberts, and the editor of the National Museum of New Zealand Records gave us permission to redraw the figure of the holotype of *P. bilaticlavia*; W. F. Hoffman and P. P. Maier made the other radiographs used in this study; J.E. Trecartin prepared the figures; F. Brigman typed the manuscript; and C. C. Baldwin, K. E. Carpenter, P. C. Heemstra, and C. D. Roberts reviewed the manuscript. The Research & Development Committee, Department of Biology, College of Charleston, provided financial assistance. This is GMBL contribution number 91.

Literature Cited

Ahlstrom, E. H., J. L. Butler, & B. Y. Sumida. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic.—Bulletin of Marine Science 26:285–402.

Anderson, W. D., Jr., N. V. Parin, & J. E. Randall. 1990. A new genus and species of anthiine fish (Pisces: Serranidae) from the eastern South Pacific with comments on anthiine relationships.—Proceedings of the Biological Society of Washington 103:922–930.

Bleeker, P. 1873. Sur les espèces indo-archipelagiques d'*Odontanthias* et de *Pseudopriacanthus.*—Nederlandsch Tijdschrift voor de Dierkinde 4: 235–240.

Fourmanoir, P. 1982. Trois nouvelles espèces de Serranidae des Philippines et de la Mer du Corail *Plectranthias maculatus, Plectranthias barroi, Chelidoperca lecromi.*—Cybium 6(4):57–64.

———, & J. Rivaton. 1980. *Plectranthias randalli* n. sp., un nouveau serranidé (anthiiné) du sud-ouest Pacifique.—Revue française d'Aquariologie 7: 27–28.

Heemstra, P. C., & W. D. Anderson, Jr. 1983. A new species of the serranid fish genus *Plectranthias* (Pisces: Perciformes) from the southeastern Pacific Ocean, with comments on the genus *Ellerkeldia.*—Proceedings of the Biological Society of Washington 96:632–637.

Hughes, D. R. 1981. Development and organization of the posterior field of ctenoid scales in the Platycephalidae.—Copeia 1981:596–606.

Johnson, G. D. 1975. The procurrent spur: an undescribed perciform caudal character and its phylogenetic implications.—Occasional Papers of the California Academy of Sciences 121:1–23.

———. 1983. *Niphon spinosus*: a primitive epinepheline serranid, with comments on the monophyly and intrarelationships of the Serranidae.—Copeia 1983:777–787.

Jordan, D. S., & B. W. Evermann. 1903. Descriptions of new genera and species of fishes from the Hawaiian Islands.—Bulletin of the United States Fish Commission 22:161–208.

Katayama, M., & H. Masuda. 1980. Two new anthiine fishes from Sagami Bay, Japan.—Japanese Journal of Ichthyology 27:185–190.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and

ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

Paulin, C. D., & C. D. Roberts. 1987. A new species of the anthiine fish genus *Plectranthias* (Percomorpha; Serranidae) from the Kermadec Islands off northern New Zealand.—National Museum of New Zealand Records 3(2):13–16.

Raj, U., & J. Seeto. 1983. A new species of the anthiine fish genus *Plectranthias* (Serranidae) from the Fiji Islands.—Japanese Journal of Ichthyology 30:15–17.

Randall, J. E. 1980. Revision of the fish genus *Plectranthias* (Serranidae: Anthiinae) with descriptions of 13 new species.—Micronesica 16:101–187.

Roberts, C. D. 1989. A revision of New Zealand and Australian orange perches (Teleostei; Serranidae) previously referred to *Lepidoperca pulchella* (Waite) with description of a new species of *Lepidoperca* from New Zealand.—Journal of Natural History 23:557–589.

Stiassny, M. L. J., & J. S. Jensen. 1987. Labroid intrarelationships revisited: morphological complexity, key innovations, and the study of comparative diversity.—Bulletin of the Museum of Comparative Zoology 151:269–319.

(WDA) Grice Marine Biological Laboratory, College of Charleston, Charleston, South Carolina 29412; (JER) Bernice Pauahi Bishop Museum, Box 19000-A, Honolulu, Hawaii 96817.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 344–350

GYMNOTHORAX PARINI, A NEW SPECIES OF MORAY EEL (TELEOSTEI: MURAENIDAE) FROM WALTERS SHOALS, MADAGASCAR RIDGE

Bruce B. Collette, David G. Smith, and Eugenia B. Böhlke

Abstract.—*Gymnothorax parini* is described from 19 specimens collected in shallow water (18 m) at Walters Shoals in the southwestern Indian Ocean. It is distinctive in having a wide bright white margin on the dorsal, caudal, and anal fins; a long anterior nostril tube that reaches or passes the edge of the upper lip when depressed ventrally; and at least half the posterior nostril located anterior to the anterior margin of the eye. It resembles several other species found around islands in the subtropical zone of the southern Indo-Pacific, but differs from all of them in color pattern, number of vertebrae (143–152), and position of the posterior nostril.

During Cruise 17 of the Soviet oceanographic research vessel *Vityaz* in December 1988, the shallow-water fish fauna was sampled with traps, fish trawls, Sigsbee trawls, and by hook and line fishing (Collette & Parin 1991). Among the fishes collected were a new species of *Scorpaenodes* described by Poss & Collette (1990) and a new moray eel, which is described herein. Walters Shoals, an isolated, submerged, oceanic mountaintop that rises to within 18 m of the surface, is located 400 nautical miles south of Madagascar and 600 nm east of South Africa at 33°09–16′S, 43°49–56′E. The purpose of this paper is to describe the new species so that the name is available for subsequent analysis of the Walters Shoals fish fauna and the other West Wind Drift islands and seamounts, and to compare it with other similar species of the genus *Gymnothorax.*

Materials and methods.—Counts and measurements follow Böhlke (1989). Material is deposited in collections of the National Museum of Natural History, Washington, D.C. (USNM); Academy of Natural Sciences of Philadelphia (ANSP); Australian Museum, Sydney (AMS); Natural History Museum of Los Angeles County (LACM); and Shirshov Institute of Oceanology, Moscow (IOAN). Other institutional acronyms follow Leviton et al. (1985).

Gymnothorax parini, new species
Figs. 1–3

Holotype.—USNM 307751 (female, 538 mm TL): western Indian Ocean, Walters Shoals; depth 18 m; *Vityaz* Cr. 17, sta. 2751, BBC 1923, 22 Dec 1988.

Paratypes.—All from Walters Shoals, 18 m, *Vityaz* Cruise 17, December 1988. ANSP 163850 (2, 545–655), same data as holotype. USNM 307749 (2, 480–590), *Vityaz* 2695a, BBC 1906, 13 Dec 1988. USNM 307750 (1, 575), *Vityaz* 2715, BBC 1914, 16 Dec 1988. USNM 307752 (4, 588–650), IOAN uncat. (3, 573–720), AMS I.28155-001 (3, 585–665), and LACM 44749-1 (3, 665–695), *Vityaz* 2683b, BBC 1901, traps, 11 Dec 1988.

Diagnosis.—*Gymnothorax parini* is distinguished from other species of the genus by the following combination of characters: anal fin with bright white distal margin and dark, unpatterned basal portion; white margin conspicuously continuous around caudal fin and on to dorsal fin, somewhat less intense anteriorly; anterior nostril very long,

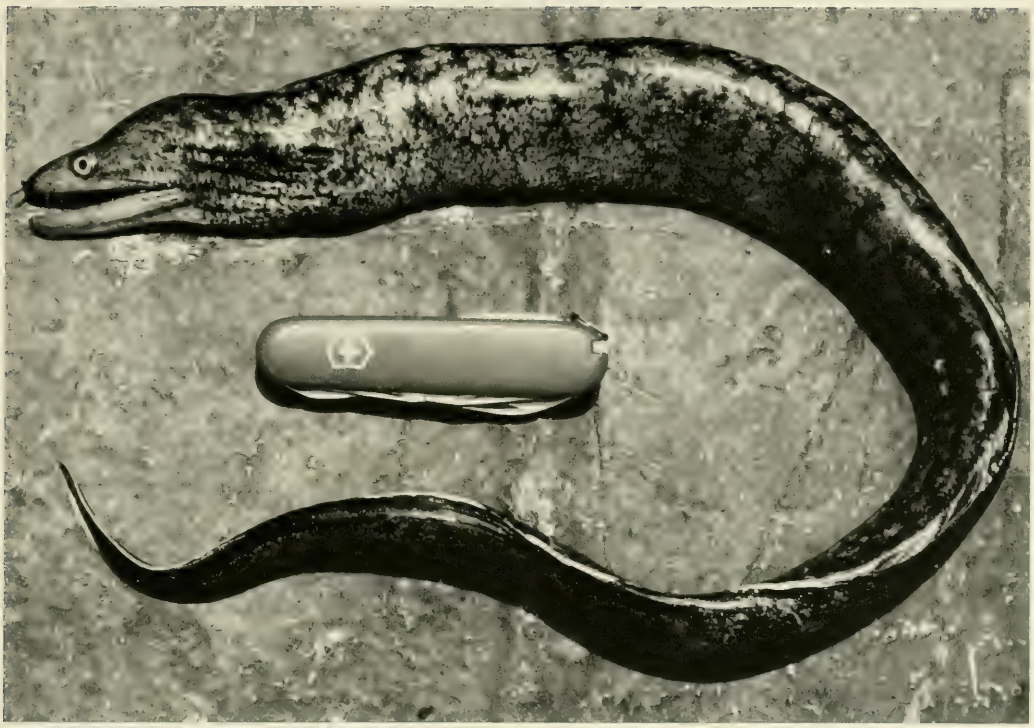


Fig. 1. *Gymnothorax parini,* new species, *Vityaz* sta. 2683. Knife is 90 mm long. (Photograph produced from color slide used for color plate Ia in Collette & Parin 1991.)

reaching upper lip when depressed ventrally; at least half of posterior nostril located anterior to vertical line through anterior margin of eye; body dark with irregular light markings; snout moderately long; all teeth uniserial; and mean vertebral formula 4-56-147.

Description.—Total vertebrae 143–152, $\bar{X}$ = 147 (n = 19), predorsal vertebrae 3–5, $\bar{X}$ = 3.8 (19), preanal vertebrae 53–58, $\bar{X}$ = 55.7 (19). Vertebral counts for holotype 4, 58, 151. Pores: branchial 2 (13), mandibular 6–7 (16), infraorbital 4 (16), supraorbital 1+2 (16). Teeth: upper jaw 6–18 (19), lower jaw 10–17 (19), median intermaxillary 1–4 (19), vomer 4–14 (16).

Proportions as % of TL: preanal 43.2–46.6 (19), predorsal 9.3–13.0 (15), head 12.4–14.7 (18), depth at anus 4.5–6.1 (16). Of head length: snout 19.1–23.3 (18), eye 7.7–11.2 (18), interorbital 10.3–14.0 (18), upper jaw 41.2–52.7 (18). Of upper jaw: snout 41.0–47.2 (19).

Body moderately elongate, typical of *Gymnothorax,* with anus slightly before midbody. Head and snout moderately elongate, jaws close completely. Dorsal fin origin immediately posterior to occiput, well anterior to gill opening. Eye moderate in size, located approximately over middle of upper jaw. Fins relatively low, dorsal somewhat higher than anal. Anterior nostril long and tubular, when depressed ventrally reaches or passes edge of upper lip. Posterior nostril without prominent raised rim, located over or slightly anterior to level of anterior margin of eye, at least half of nostril anterior to vertical line with anterior margin of eye.

Pores in lateralis system small and inconspicuous and arranged in typical *Gymnothorax* pattern (Fig. 2). Two in branchial section of lateral line, anterodorsal to gill

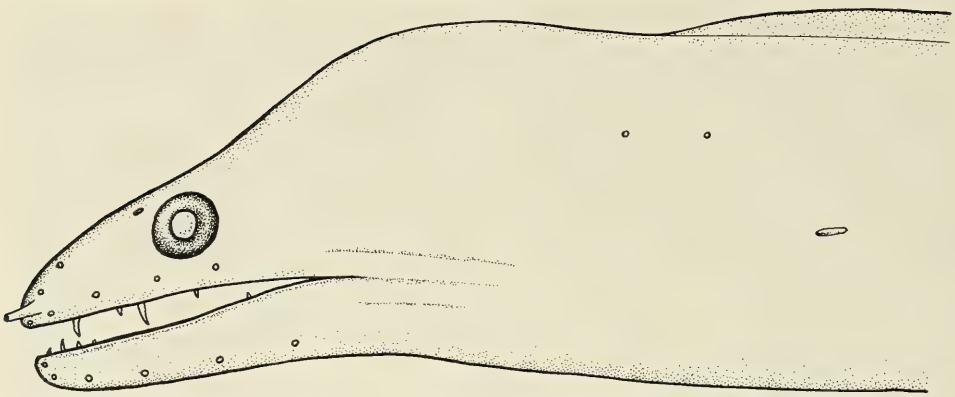


Fig. 2. Lateral view of head of holotype of *Gymnothorax parini,* new species (USNM 307751, 538 mm TL) to show cephalic lateral line pores.

opening. Six pores in mandibular canal (one specimen with seven on one side), all anterior to rictus. All four pores in infraorbital canal located along upper jaw between anterior nostril and vertical with posterior margin of eye. Three supraorbital pores: one (ethmoidal pore) at tip of snout on edge of upper lip, one adjacent to base of anterior nostril, and one posterodorsal to anterior nostril.

All teeth smooth, without serrations of any kind (Fig. 3). Lateral teeth in upper jaw narrowly triangular, slightly compressed, somewhat recurved, and uniserial; maxillary and intermaxillary series confluent, without obvious demarcation. Peripheral intermaxillary teeth increase in size from anterior to posterior; anterior maxillary teeth approximately same size as posterior intermaxillary teeth, becoming progressively smaller posteriorly and also somewhat more steeply inclined in posterior direction. A few tiny teeth set immediately before and/or behind large intermaxillary teeth. One to four large, slender, sharply pointed, depressible fangs on midline of intermaxillary plate, increasing in size from anterior to posterior. Teeth in lower jaw similar in size and arrangement to those of upper jaw, largest anteriorly and decreasing in size posteriorly; a few tiny teeth set between large anterior teeth. Vomerine teeth small, triangular, pointed, mainly uniserial but occasionally one or two teeth displaced to side. Clear difference between males and females in number of teeth (Table 1), with males having fewer upper-jaw, lower-jaw, and median intermaxillary teeth.

Ground color in alcohol dark brown, almost black, overlain with irregular, light brown markings with erratic borders and mottled within by darker brown. Intensity and extent of light markings variable; some specimens nearly uniformly black, others with extensive light areas, but overall impression dark with light markings. Pale areas sometimes form irregular bars, sometimes snowflake- or lichen-like patches. Head usually lighter than body, without patchwork pattern of light markings, often irregularly mottled with darker brown. Anal fin marked conspicuously with bright white margin, which has a bluish cast in life; basal part of fin uniformly dark brown or black, without markings. Dorsal fin colored similarly, but narrower white edge tends to be interrupted anteriorly in smaller specimens; basal part of dorsal fin dark, but some light markings encroach upon it from body. White margin conspicuous around caudal fin. Skin

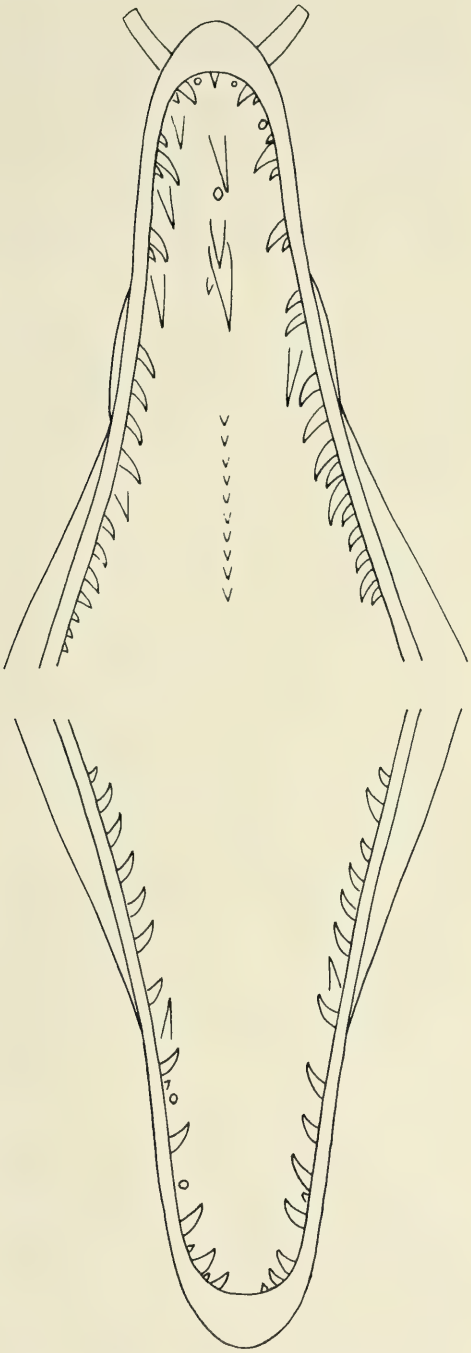


Fig. 3. Dentition of holotype of *Gymnothorax parini*, new species (USNM 307751, 538 mm TL).

Table 1.—Number of teeth in male and female *Gymnothorax parini*, expressed as total number, right + left, in upper and lower jaws (number of specimens in parentheses).

	Upper jaw	Lower jaw	Median intermaxillary
Females	30–32 (5)	29–32 (4)	3–4 (5)
Males	19–26 (8)	24–30 (7)	1–2 (8)

immediately around gill opening tends to be dark, but without conspicuous spot around it. Some dark pigment at corner of mouth, but not forming a conspicuous spot. Sensory papillae on head small, each set in a tiny dark spot, forming inconspicuous pattern of rows.

Sex and sexual dimorphism.—Of the 19 specimens of *Gymnothorax parini*, five, including the holotype, are clearly females (538–650 mm TL), eight are males (480–720 mm), and the sex of three was not determined. Although the ovaries are enlarged and the eggs conspicuous, none of the females is in spawning condition. At least four other species of *Gymnothorax* show a similar sexual dimorphism in the number of teeth as reported here for *G. parini*: *G. richardsoni* (Hatooka 1986), *G. enigmaticus* and *G.* cf. *monochrous* (M. A. Gibbs, pers. comm.), and *G. chilospilus* (D. G. Smith, work in progress). Hatooka also reported dimorphism in the dentition of two species of *Echidna*, and Gibbs has found another case in *Enchelycore schismatorhynchus*. Sexual dimorphism in tooth number may be widespread among morays and deserves further study. In the case of *G. chilospilus*, the female tooth pattern is also the juvenile pattern; the males change at maturity. With material available, we cannot determine whether *G. parini* follows the same pattern.

Aberrant specimen.—Of the 20 specimens of *Gymnothorax* collected at Walters Shoals, one (USNM 307753, *Vityaz* station 2695) stands apart from the others in sev-

eral ways. The most striking difference is the low number of vertebrae, 4-52-132. The total is 11 vertebrae fewer than for any of the *G. parini* and 15 fewer than the mean value for 19 specimens. If an eel loses part of its tail, it will regenerate a caudal fin, but this new structure never looks exactly like the original. If this specimen had lost 10–15 caudal vertebrae, it would be obvious from the radiograph, but this specimen shows no evidence of a regenerated caudal fin; the entire caudal skeleton appears perfectly normal. The specimen further differs from the others in color. Whereas *G. parini* were very dark, nearly black, when freshly collected, this specimen was distinctly brown. Even in preservative this difference is apparent. In addition, unlike in *G. parini,* there is a small but distinct dark spot around the gill opening, and the grooves around the neck and throat are streaked with darker brown. Finally, the upper jaw length and interorbital width are slightly higher than comparable values noted in *G. parini,* and the snout length as percent of upper jaw length is less in this specimen.

We do not know how to interpret this specimen. It is sufficiently distinct from the others that we have excluded it from the type series, yet with only one specimen we hesitate to describe it as a second species. We leave the problem unresolved for the time being and provide some counts and measurements: USNM 307753, male, 570 mm TL, preanal 265 mm (46.5% TL), predorsal 65 mm (11.4% TL), head 76 mm (13.3% TL), depth at anus 34 mm (6.0% TL), snout 16.3 mm (21.5% HL, 37.9% upper-jaw length), eye 8.2 mm (10.8% HL), interorbital 11.1 mm (14.6% HL), anterior nostril 3.7 mm (4.9% HL), vertebrae 4-52-132, cephalic pores as in *G. parini.* Teeth damaged, approximately 16 on left side of upper jaw and 11+ on right; 20 teeth on right side of lower jaw, left side too damaged to count; median intermaxillary teeth 2; vomerine teeth 8.

Distribution.—Known only from Walters Shoals in the southwestern Indian Ocean. Collected from depths of 18 m by traps and by hook and line. No morays have been reported from any of the other six islands and seamounts extending along the West Wind Drift between Gough and Tristan da Cunha in the South Atlantic to Amsterdam and St. Paul in the southwestern Indian Ocean.

Etymology.—Named in honor of our distinguished colleague Nikolai Parin, an expert on the fish fauna of seamounts and scientific leader of cruise 17 of the *Vityaz,* on which all the material of this species was collected.

Comparisons.—*Gymnothorax parini* is one of several similar species occurring around islands in the subtropical zone of the southern Indo-Pacific region that have a prominent white margin on the anal fin and sometimes on the dorsal fin.

Gymnothorax woodwardi McCulloch, from Western Australia, is the closest geographic neighbor of *G. parini,* and the only species in this group that is known from the Indian Ocean. Unlike *G. parini, G. woodwardi* has the posterior nostril entirely posterior to a vertical line through the anterior margin of the eye. The color pattern of this species differs in that the trunk pigmentation consists of dark reticulations on a lighter background, confined mainly to the dorsal half, changing to a series of irregular bar-like markings on the tail. The white margin is prominent on the anal fin and on most of the dorsal fin, but the submarginal dark band is only weakly developed. There are 132–139 vertevrae. Two syntypes (AMS I.12224–5) have 4 predorsal, 56–58 preanal, and 135–137 total vertebrae, MVF 4-57-136.

Gymnothorax annasona Whitley occurs at Lord Howe Island and Middleton Reef, both on the Lord Howe Rise. Its snout is somewhat shorter and deeper than that of *G. parini,* the anterior nostril is slightly

shorter, and the posterior nostril is located entirely over the eye. The basal part of the anal fin is patterned, and the body color is different, consisting of moderately large spots separated by a densely speckled matrix. The holotype (AMS IA.6867) has 58 preanal and 133+ total vertebrae (tail tip missing); two other specimens have 4, 56–57, 141–143.

Gymnothorax nubilus (Richardson), from Norfolk Island, differs primarily in color. Its body is brown (a rich, chestnut color in the small specimen examined by us) with irregular cloud-like markings of darker brown, more or less conspicuous. There are three conspicuous dark streaks on the throat, the dorsal one running posteriorly from the corner of the mouth; a midventral streak is also present. The dorsal and anal fins have a dark submarginal band basal to the white edge. The holotype (BMNH 1972.1.26.159) has 3-52-132 vertebrae. Ayling & Cox (1982: 92, pl. 6) reported this species from northern New Zealand, but their description and illustration suggest that it may not be identical to the *G. nubilus* of Richardson.

Gymnothorax eupterus (Günther), from Raoul Island in the Kermadecs, was described as having white-margined fins and "gular folds and angle of the mouth dark brown" (Günther, 1870:123). The holotype (BMNH 1855.8.16.50) has 4-52-134 vertebrae. This seems very similar to *G. nubilus.*

Gymnothorax nasuta De Buen is known from Easter and Pitcairn islands (Randall & McCosker 1975:28). It has a shorter and less slender snout than *G. parini* and fewer vertebrae (138–139, Randall & McCosker 1975: 23). The white margin is weakly developed on the dorsal fin and around the end of the tail. The basal parts of both fins are patterned. The body is dark and speckled with small, irregular white spots, sometimes forming poorly defined patches.

Gymnothorax bathyphilus Randall & McCosker, from 250 m off Easter Island, is light yellowish gray, with faint darker reticulations and blotches. There is a submarginal dark band on both dorsal and anal fins, but basally both fins are patterned. The dorsal profile of the snout is flatter than that of *G. parini,* which tends to be slightly convex.

Two specimens from Juan Fernandez Island (USNM 88679 and 88680, 810 and 824 mm TL) closely resemble *G. bathyphilus* but they are dark brown instead of light gray, with a few indistinct darker spots on the dorsal part of the body and darker streaks on the throat. Both specimens have fewer teeth in the upper and lower jaws than the type of *G. bathyphilus* (13–16 vs. 20–22 respectively in the upper, and 15–17 vs. 21–23 in the lower). The one intact specimen has 149 vertebrae vs. 145 in the type of *G. bathyphilus.*

One northern hemisphere subtropical species, *Gymnothorax kidako* (Schlegel) from Japan, resembles *G. parini* in body color and white-margined anal fin. In this species, however, the snout is slightly shorter, the anterior nostril is located entirely over the eye, and there are 142 vertebrae in the specimens radiographed.

Several other species have white-margined anal fins, but they either lack a white-margined dorsal fin or they have other characters that readily separate them from *G. parini.*

Of all the preceding species, *Gymnothorax parini* seems most similar to *G. nubilus* and *G. bathyphilus.* These have the most slender snouts and the most prominent white margins on the fins. Both have dark submarginal bands on the fins immediately basal to the white margins, though narrower than that of *G. parini,* which covers the entire basal portion of the anal fin. Moreover, both species have long anterior nostrils that reach the edge of the upper lip, and both have the posterior nostril located over or anterior to the anterior margin of the eye. In addition, all three have the small sensory papillae on the head set in tiny black spots

forming patterns of rows, although these are somewhat less prominent in *G. parini* than in the others.

None of the above species extends into the tropical zone and, except for *Gymnothorax woodwardi,* none occurs on the margins of continents. They seem to be elements of a fauna peculiar to subtropical islands of the southern Indo-Pacific. This whole area has been poorly sampled using methods likely to capture these eels (traps, hook and line in moderately deep water), therefore any general conclusions on biogeography would be premature. We suggest that these islands and reefs would be promising areas for future investigation.

Comparative material.—*Gymnothorax annasona*: AMS IA.6867 (holotype, 500 mm TL), Middleton Reef. AMS 17369-006 (1, 485), BPBM 1477 (1, 540), BPBM 14838 (1, 340), Lord Howe Island. *Gymnothorax* cf. *bathyphilus*: USNM 88679 (1, 810) and USNM 88680 (1, 824), Juan Fernandez Is. *Gymnothorax kidako*: USNM 71825 (1, 445) and USNM 71826 (1, 540), Misaki, Japan. *Gymnothorax nasuta*: USNM 65521 (1, 652), Easter Island. *Gymnothorax nubilus*: NMNZ P.11717 (1, 287), Norfolk Island. *Gymnothorax woodwardi*: WAM 13263 (holotype, 515), Houtmans Abrolhos, Western Australia. WAM 27949-021 (3, 129–228), Jurien Bay, Western Australia. WAM 28523-001 (1, 385), Augusta, Western Australia.

Acknowledgments

N. V. Parin kindly invited B. B. Collette to participate in the cruise of the *Vityaz* that resulted in collecting the material of this new species of *Gymnothorax*. J. R. Paxton and his staff at the AMS made material available for examination and had the holotype of *Gymnothorax annasona* x-rayed. J. E. Randall (BPBM), C. Roberts (NMNZ), and J. B. Hutchins (WAM) loaned us additional comparative material. M. A. Gibbs (Moss Landing Marine Laboratory) kindly shared her unpublished information on sexual dimorphism in muraenid dentition. Figures 2 and 3 were drawn by Keiko Hiratsuka Moore. Drafts of the manuscript were read by T. A. Munroe and A. B. Williams.

Literature Cited

Ayling, T., & G. J. Cox. 1982. Collins guide to the sea fishes of New Zealand. Collins: Auckland, Sydney, London, 343 pp.

Böhlke, E. B. 1989. Methods and terminology. *In* Fishes of the western North Atlantic.—Sears Foundation for Marine Research Memoir 1, Part 9:1–7.

Collette, B. B., & N. V. Parin. 1991. Shallow-water fishes of Walters Shoals, Madagascar Ridge.—Bulletin of Marine Science 48:1–22.

Günther, A. 1870. Catalog of fishes in the British Museum, vol. 8, 549 pp.

Hatooka, K. 1986. Sexual dimorphism found in teeth of three species of moray eels.—Japanese Journal of Ichthyology 32:379–385.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology: part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

Poss, S. G., & B. B. Collette. 1990. *Scorpaenodes immaculatus,* a new species of scorpionfish (Osteichthyes: Scorpaenidae) from Walthers Shoals, ings of the Biological Society of Washington 103: 543–549.

Randall, J. E., & J. E. McCosker. 1975. The eels of Easter Island with a description of a new moray.—Contributions in Science, Natural History Museum of Los Angeles County 264:1–32.

(BBC) National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, D.C. 20560; (DGS) Division of Fishes, National Museum of Natural History, Washington, D.C. 20560; and (EBB) Academy of Natural Sciences, 19th & the Parkway, Philadelphia, Pennsylvania 19103.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 351–355

GEOGRAPHIC DISTRIBUTION OF *MICRONYCTERIS SCHMIDTORUM* SANBORN (CHIROPTERA: PHYLLOSTOMIDAE)

César F. Ascorra, Don E. Wilson, and Alfred L. Gardner

Abstract.—Specimens of *Micronycteris schmidtorum* Sanborn from Brazil and Perú extend the distribution of the species from the previously known southernmost records in Venezuela. Preliminary data suggest geographic variation in size, with larger individuals in the north and smaller ones in the south.

Micronycteris schmidtorum Sanborn, 1935 (Fig. 1), is known from southern México to Venezuela (Villa-R. 1966, Eisenberg 1989), although no specimens have been recorded from eastern Panamá or Colombia. Throughout this range the species has been found in association with humid habitats where it forages for insects and fruit (Wilson 1973, Gardner 1977, Eisenberg 1989). It also occurs in multistratal tropical evergreen forest and dry thorn forest (Handley 1976), but is uncommon in both. Most specimens have been taken from roosts in hollow trees (Handley 1976).

In April 1977, M. R. Willig collected three specimens of *Micronycteris schmidtorum* from two localities in semiarid Caatinga habitat near Exu, Pernambuco, Brazil. These specimens were among those reported as *Micronycteris* sp. by Mares et al. (1981). In March 1978, we collected two specimens in mist nets in eastern Brazil (Fig. 2). The first was taken in humid forest at the Estacão Ecológica do Tapacurá, São Lourenço da Mata, Pernambuco, at an elevation of 170 m. The second was taken from Sitio Luanda, Itaitera, Crato, Ceará, in the vicinity of a stream in humid second-growth forest habitat below dry Cerrado habitat. These specimens represent the first records of the species from Brazil. These sites are approximately 3200 km southeast of Río Mavaca, Territorio Federal Amazonas, Venezuela, previously the southernmost recorded location for the species.

In March 1990, we netted a male in secondary tropical humid forest at the Centro de Investigación Jenaro Herrera, Requena, Loreto, Perú. This is the first Peruvian record and represents an extension of the range 1200 km from the Venezuelan locality. Requena is approximately 4000 km west of the Brazilian localities.

The Brazilian and Peruvian specimens average smaller in size in almost all dimensions when compared with specimens from more northern localities (Table 1). The two Guatemalan specimens (the holotype and a topotype) are larger than any of the other specimens we examined. Specimens from Costa Rica (Fig. 1), Panamá, and Venezuela are intermediate in size. Additional samples from the southern part of the range in Perú and Brazil might clarify the nature of this geographic variation.

The most recent list of Peruvian bats (Graham & Barkley 1984) listed 131 species. Pacheco et al. (1991) added six species; *Micronycteris schmidtorum* brings the total to 138.

The three species of small *Micronycteris* (*Micronycteris*) that are most easily misidentified are *M. megalotis, M. minuta,* and *M. schmidtorum.* Although similar in size and cranial features, and having a medial "notch" in the band of skin connecting the ears, each species can be distinguished on the basis of ventral color pattern, depth of notch in the band between ears, length of calcar, length of uropatagium relative to tail,

Fig. 1. *Micronycteris schmidtorum* from Costa Rica (Photograph by Barbara L. Clauson).

and relative size of lower premolars. *Micronycteris schmidtorum* has a grayish-white venter, a moderately notched band between ears, uropatagium more than twice length of tail, calcar longer than foot, and first lower premolar (p2) distinctly larger than second (p3). *Micronycteris megalotis* is similar to *M. schmidtorum* in length of calcar and uropatagium, but has a brownish venter, a shallow notch in the band between ears, and lower premolars that are about equal in size. *Micronycteris minuta* can be identified by

Table 1.—Means (±one standard deviation) of measurements of specimens of *Micronycteris schmidtorum* (*n* = sample size). Measurements for Guatemala specimens from Sanborn (1935:81).

Measurement	Guatemala	Costa Rica	Panama	Venezuela	Brasil	Peru
Total length	65.50 ± 2.12	61.00	60.00 ± 3.74	63.30 ± 2.07	56.50 ± 0.71	56.00
	n = 2	*n* = 1	*n* = 4	*n* = 6	*n* = 2	*n* = 1
Tail length	15.00 ± 2.82	9.00	11.50 ± 2.38	15.83 ± 1.84	12.00 ± 0	13.00
	n = 2	*n* = 1	*n* = 4	*n* = 6	*n* = 2	*n* = 1
Hind foot length	10.00 ± 0	11.00	9.25 ± 0.96	10.83 ± 0.98	9.00 ± 0	8.00
	n = 2	*n* = 1	*n* = 4	*n* = 6	*n* = 2	*n* = 1
Ear length	17.00 ± 1.41	19.00	19.13 ± 1.65	21.50 ± 1.23	20.50 ± 0.71	18.00
	n = 2	*n* = 1	*n* = 4	*n* = 6	*n* = 2	*n* = 1
Forearm length	35.30 ± 0.14	33.00	34.16 ± 0.45	35.14 ± 1.45	33.85 ± 0.35	31.60
	n = 2	*n* = 1	*n* = 5	*n* = 6	*n* = 2	*n* = 1
Tibia length	16.40 ± 0.14	15.15	15.24 ± 0.84	16.23 ± 0.46	13.70 ± 0.71	14.00
	n = 2	*n* = 1	*n* = 5	*n* = 6	*n* = 2	*n* = 1
Calcar length	12.15 ± 0.21	11.35	11.37 ± 0.26	11.00 ± 0.51	10.28 ± 0.88	11.15
	n = 2	*n* = 1	*n* = 5	*n* = 6	*n* = 2	*n* = 1
Skull length	20.55 ± 0.07	19.80	19.53 ± 0.20	19.50 ± 0.35	18.15 ± 0.90	17.70
	n = 2	*n* = 1	*n* = 5	*n* = 6	*n* = 2	*n* = 1
Condylobasal length	17.90 ± 0.14	17.50	17.31 ± 0.13	17.47 ± 0.43	16.08 ± 1.31	15.60
	n = 2	*n* = 1	*n* = 4	*n* = 6	*n* = 2	*n* = 1
Maxillary toothrow L.	7.85 ± 0.07	7.50	7.44 ± 0.11	7.56 ± 0.24	6.53 ± 1.03	6.50
	n = 2	*n* = 1	*n* = 6	*n* = 6	*n* = 2	*n* = 1
Mastoid breadth	9.05 ± 0.21	9.05	8.75 ± 0.11	8.71 ± 0.20	8.50 ± 0.35	8.15
	n = 2	*n* = 1	*n* = 5	*n* = 6	*n* = 2	*n* = 1
Interorbital breadth	4.30 ± 0	4.20	4.26 ± 0.09	4.18 ± 0.15	4.13 ± 0.18	3.95
	n = 2	*n* = 1	*n* = 6	*n* = 6	*n* = 2	*n* = 1
Zygomatic breadth	9.10 ± 0.21	9.00	9.06 ± 0.20	9.01 ± 0.28	8.80	8.50
	n = 2	*n* = 1	*n* = 5	*n* = 4	*n* = 1	*n* = 1

its white venter, deep notch in the band between ears, calcar shorter than foot, uropatagium less than twice length of tail, and first upper premolar (P3) shorter than second (P4). Upper premolars are about the same height in the other two taxa.

Specimens examined.—(USNM = National Museum of Natural History, Washington, D.C.; MUSM = Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Perú; CM = Carnegie Museum of Natural History, Pittsburgh, PA). Belize: Toledo, Big Fall Village, 0.5 mi. E Rio Grande Bridge (♂-CM 90108). Costa Rica: Heredia, Parque Nacional Braulio Carrillo, 11 km S, 4.5 km W Puerto Viejo, 300 m (♀-USNM 562753). Panamá: Canal Zone, Barro Colorado Island (♀-USNM 534826); Canal Zone, Península Bohio (♀-USNM 536969, ♀-454887); Chiriquí, Cerro Punta (♀-USNM 314208); Los Santos, Las Palmitas (♀-USNM 323061). Venezuela: Falcón Capatárida (♂-USNM 444235); Territorio Federal Amazonas, Río Mavaca, 108 km SSE Esmeralda (♀-USNM 388713); Territorio Federal Amazonas, Belén, Río Cunucunuma (♀-USNM 388704); Territorio Federal Amazonas, San Juan, Río Manapiare (♀-USNM 407257, ♂-USNM 407258, ♂-USNM 407259). Brazil: Pernambuco, Tapacurá, São Lourenço da Mata (♂-USNM 555703); Pernambuco, Fazenda Alto do Ferreira, 5 km SW Exu (2♂-CM 98908, 98909); Pernambuco, Fazenda Cantareno, 4.5 km NNE Exu (♂-CM 98910); Ceará, Sitio Luanda, Itaitera, Crato

Fig. 2. Geographic distribution of *Micronycteris schmidtorum*.

(♀-USNM 555702). Perú: Loreto, Requena, Jenaro Herrera (♂-MUSM 5528).

Acknowledgments

The field work in Perú was supported by a grant from U.S.A.I.D. to D. L. Gorchov. We are grateful to C. O. Handley, Jr., for commenting on an earlier version of the manuscript, and to D. A. Schlitter for allowing us to examine specimens in the collection of the Carnegie Museum of Natural History. We thank the Office of Fellowships and Grants of the Smithsonian Institution for supporting Ascorra's work in the National Museum of Natural History Collections. B. L. Clauson kindly provided the photograph in Fig. 1. This is contribution No. 10 of the Smithsonian Institution's Biological Diversity in Latin America Program.

Literature Cited

Eisenberg, J. F. 1989. Mammals of the Neotropics. The northern Neotropics. Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, 1:1–499.

Gardner, A. L. 1977. Feeding habits. Pp. 293–350 *in* R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds., Biology of the bats of the New World family Phyllostomatidae. Part II.—Special Publications, The Museum, Texas Tech University 13:1–364.

Graham, G. L., & L. J. Barkley. 1984. Noteworthy records of bats from Peru.—Journal of Mammalogy 65:709–711.

Handley, C. O., Jr. 1976. Mammals of the Smithsonian Venezuelan Project.—Brigham Young University Science Bulletin, Biological Series 20(5):1–91.

Mares, M. A., M. R. Willig, K. E. Streilein, & T. E. Lacher, Jr. 1981. The mammals of northeastern Brazil: a preliminary assessment.—Annals of Carnegie Museum 50:81–137.

Pacheco, V., H. de Macedo, E. Vivar, C. Ascorra, &

R. Arana. 1991. Lista anotada de los mamíferos Peruanos.—Publicaciones del Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (in press).

Sanborn, C. C. 1935. New mammals from Guatemala and Honduras.—Field Museum of Natural History, Zoological Series 20:81–85.

Villa-R., B. 1966 [1967]. Los murciélagos de México. Universidad Nacional Autónoma de México, Instituto de Biologia, México, 491 pp.

Wilson, D. E. 1973. Bat faunas: a trophic comparison.—Systematic Zoology 22:14–29.

(CFA) Departamento de Mastozoología, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Apartado 140434, Lima 14, Perú; (DEW) Neotropical Biodiversity Program, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (ALG) Biological Survey, NERC, U.S. Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 356–369

A NEW SUBSPECIES OF THE DOUBLE-CRESTED CORMORANT, *PHALACROCORAX AURITUS,* FROM SAN SALVADOR, BAHAMA ISLANDS

George E. Watson, Storrs L. Olson, and J. Robert Miller

Abstract.—An isolated population of Double-crested Cormorants, apparently endemic to the extensive system of saline lakes on the island of San Salvador in the Bahamas, is described as a new subspecies, *Phalacrocorax auritus heuretus,* that is smaller than the smallest mainland subspecies, *P. a. floridanus.* The reduced size of the San Salvador cormorants may be an adaptation to the small size of the local fishes that constitute its prey. The total population of *P. a. heuretus* on San Salvador is probably less than 600. Breeding records of *P. auritus* and *P. brasilianus* in the Bahamas and West Indies are reviewed.

An undescribed population of cormorant breeds in mangroves around Great Lake on San Salvador Island, Bahamas. Specimens were first collected 104 years ago, but since then there has been much confusion about their specific identification. Two species of cormorants occur in the southeastern United States and the northern Caribbean (Clapp et al. 1982). The larger, more northern, Double-crested Cormorant, *Phalacrocorax auritus,* and the smaller, more southern, Olivaceous Cormorant *P. brasilianus,* differ strikingly in plumage during courtship, but after incubation the "nuptial plumes" are dropped and both species are essentially all black. None of the specimens of cormorant from San Salvador is in courtship plumage, however, and the diminutive size of the birds, without consideration of other characters, has almost universally led investigators to identify them as *P. brasilianus.* (For use of the specific name *P. brasilianus* rather than *P. olivaceus,* the name in general use in recent U.S. publications, see Browning [1989].)

San Salvador (formerly Watling or Watling's Island, the names found generally in the ornithological literature), best known for reputedly being the site of Columbus' first New World landfall (Richardson & Goldsmith 1987), is the easternmost of the northern Bahamas (Fig. 1). It is composed entirely of raised coral and lies at 24°02′N, 74°28′W, east of the Great Bahama Bank, of which it never formed a part, even during glacial maxima of the Pleistocene, when sea levels were significantly lower. San Salvador is about 10 × 23 km and 156 km^2 in area, with an elevation of about 43 m at its highest point. Although formerly completely converted to agriculture, the predominant vegetation is now dense, semideciduous scrub. The main physiographic features of San Salvador are the many hypersaline interior lakes, the largest of which is Great Lake. Inland waters constitute about one third of the surface area of the island. Mangrove swamps occur chiefly on the fringes of the saline lakes and ponds.

Our interest in this problem was aroused when Miller, who was uncertain about identification of the San Salvador cormorant, with his student Hans Gabler, collected two adult specimens in 1978, which were sent frozen to the Smithsonian and were routinely prepared as study skins (USNM 582413–582414). Because the specimens were small, with short tails and anomalous facial characteristics, we suspected that they might represent a new form of *P. brasilianus*

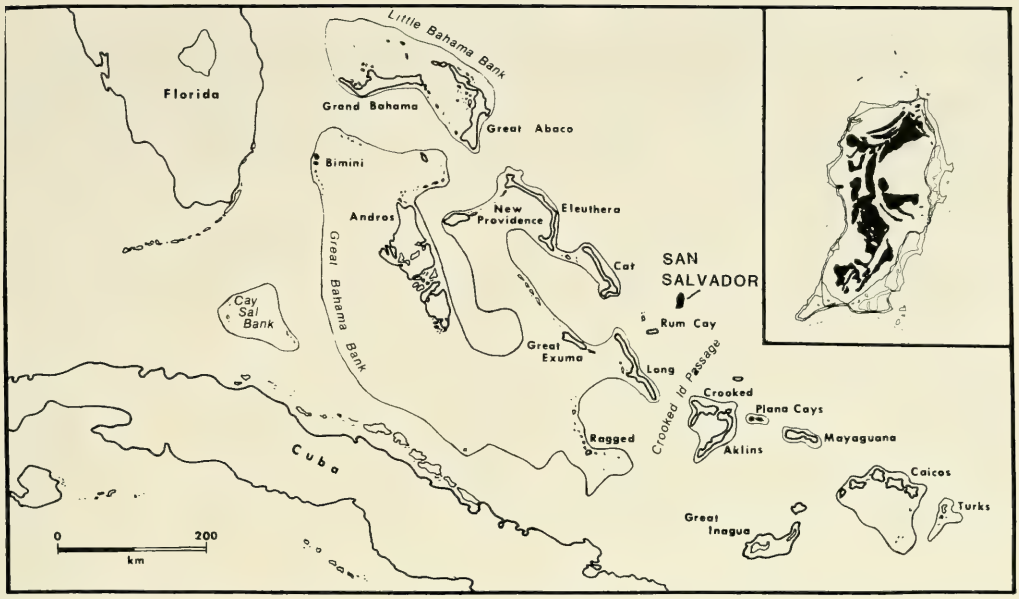


Fig. 1. Map of the Bahamas showing the position of San Salvador and the extensive system of shallow banks (contour line = 50 fathoms [91 m]). Inset: Map of San Salvador showing extent of the inland lakes in black.

having some of the characteristics of *P. auritus.*

Subsequent study of all previously-taken museum specimens from San Salvador in United States collections, as well as a more recently collected series of skins and skeletons, showed, on the contrary, that the interior lakes harbor an undescribed diminutive form of *P. auritus,* markedly smaller than the small southeastern race, *P. a. floridanus.*

The nomenclatural history of the San Salvador cormorant is less complicated than it might be because the island does not figure prominently in the ornithological literature and few specimens have been collected. Ridgway (1891) reported two cormorants taken on San Salvador on 1 March 1886 during a U.S. Fish Commission cruise aboard the "Albatross" (USNM 108821–108822). One of these he identified as *P. mexicanus* (=*P. brasilianus*) and the other as *P. dilophus* (=*auritus*) *floridanus.* Cory (1892a), reporting on a collection from San Salvador made in fall 1891, recorded eight specimens of *P. dilophus floridanus,* four of which are still in the Field Museum of Natural History in Chicago (FMNH 96432–96433, 96439–96440). In his list of West Indian birds, however, Cory (1892b:85) cited both species for the island, presumably on the authority of Ridgway.

Riley (1905a, 1905b) visited San Salvador from 11 to 13 July 1903 and reported a colony of cormorants, under the name *P. vigua mexicanus,* breeding in tall mangroves. Although he claimed to have shot cormorants, none were catalogued into the Smithsonian collection with his other specimens from San Salvador. Worthington visited San Salvador on 10 March 1909 and collected an immature cormorant (CMNH 30908) that was identified as *P. brasilianus* (Todd & Worthington 1911). Paulson (1966) recorded Olivaceous Cormorants nesting on San Salvador in late December 1965, based on three specimens he collected that are now in the Schwartz-Klinikowski collection in the Museum of Zoology, Louisiana State University (originally SK 6653–6655, now LSUMZ 141214–141216). The most recent report is that of Miller (1978), who, on the

Table 1.—Measurements of various cormorant populations.

Population	Sex	Wing (mm)			Tail (mm)			T/W ratio	
		n	Range	Mean	*n*	Range	Mean	*n*	Range
P. brasilianus	male	10	257–272	(265.6)	10	147–165	(155.5)	10	0.56–0.62
Texas	female	8	251–265	(257)	8	140–162	(145.8)	8	0.54–0.61
P. brasilianus	male	2	260, 263		2	151, 165		2	0.58, 0.62
Cuba	female	4	237–245	(242)	4	137–149	(143.8)	4	0.56–0.61
P. a. heuretus	male	8	260–280	(270.6)	8	123–132	(128.3)	8	0.45–0.49
San Salvador	female	8	259–276	(263.1)	7	117–132	(121.9)	7	0.45–0.48
P. a. heuretus	male	2	272, 277		2	131, 140		2	0.50, 0.51
Grand Bahama	female	1	260		1	120		1	0.46
P. a. floridanus	male	32	282–316	(303.1)	30	130–157	(144.3)	30	0.45–0.51
Florida	female	17	275–305	(288.9)	15	125–152	(135.5)	15	0.45–0.51
P. a. floridanus	male	4	290–307	(299.3)	4	140–154	(145.5)	4	0.46–0.50
Cuba	female	11	262–305	(286.6)	9	123–158	(139.2)	9	0.45–0.52
P. a. floridanus	male	4	305–320	(311.3)	3	151–165	(156.3)	3	0.50–0.53
Grand Bahama Andros Great Sal	female	4	285–285	(285)	3	130–141	(135.8)	3	0.46–0.49

basis of observations during five visits between 1973 and 1976, recorded Olivaceous Cormorants breeding on Great Lake, although he was not certain of their specific identity.

Handbook and checklist coverage of the San Salvador cormorant has been varied. Hellmayr & Conover (1948:139–140) cite Cory's four specimens from the "Interior Lake, San Salvador" under *P. a. floridanus,* but give the breeding range of that species as being "on some of the Bahama Islands (Great Abaco, Andros, Bimini, etc.), in Cuba (formerly) and on the Isle of Pines," without mentioning San Salvador. Under *P. brasilianus* they give the breeding range as being "in the Bahama Islands (Watling's Island), Cuba and the Isle of Pines," but they list no Field Museum specimens from the Bahamas. Bond (1956:7–8) cites *P. auritus floridanus* from ten Bahaman islands, including Watling [sic], and implies, but does not specifically indicate, breeding. Under *P. brasilianus mexicanus,* he lists only Watling's Island in the Bahamas and adds, parenthetically, "found breeding." Bond (1980) states that "*P. olivaceus* [=*brasilianus*] is known to breed on San Salvador and Great Inagua, and there is probably a colony on Cat Island (J. Robert Miller in litt). The larger *P. auritus* supposedly nests on some of the northernmost Bahamas, but definite information is lacking." The fifth edition of the A.O.U. Check-list (1957:36–37) and the revised first volume of Peters' Check-list (Dorst & Mougin 1979:170) essentially paraphrase Bond (1956). The A.O.U. Check-list, sixth edition (1983:38–39), also mentions that the Olivaceous Cormorant is "resident" on Cat Island and Great Inagua in the Bahamas.

Olivaceous Cormorants from Cuba, Texas, Mexico, and northern Central America (*P. brasilianus mexicanus*) are smaller than any of the currently recognized forms of the Double-crested Cormorant, there being no overlap in wing length (Table 1) between *P. brasilianus* and *P. auritus floridanus,* the smallest form of that species hitherto known. Bill size is likewise small in *P. brasilianus.* This general indication of overall size is what has led to misidentification of specimens of cormorants from San Salvador as *P. brasilianus.*

Plumage and facial characters, however, are more reliable for separating the two spe-

Table 1.—Extended.

Culmen (mm)			Tarsus (mm)			Mid toe (mm)		
n	Range	Mean	*n*	Range	Mean	*n*	Range	Mean
9	46–40	(47.5)	10	48.5–53	(51.3)	10	67–72	(70.6)
7	42.5–47	(44.5)	8	46–57	(50.5)	8	67–70	(68.4)
2	47, 48		2	47.5, 52		1	70.5	
4	41–47	(44.1)	4	47–50	(47.9)	2	70, 71	
5	43.5–49	(45.8)	5	49–57	(53.6)	3	68–72.5	(70)
5	43–49.5	(45.2)	5	51–54	(53.1)	4	66–75	(70.1)
1	48		2	52, 60		2	71, 81.5	
1	42		1	50		1	67	
32	47–61	(56.5)	32	57.5–66.5	(62.6)	29	83–98	(93.3)
19	51–60	(54.6)	19	56–66	(60.6)	18	77–93	(87.6)
4	53–59	(56.8)	4	60–66	(62)	4	84–97	(91.3)
11	44.4–58	(53)	11	55.5–65	(60.5)	10	75–93	(83.5)
4	55–60	(57.6)	2	62, 65		1	90	
3	54–57	(55.1)	3	59–60	(59.3)	3	78–82	(81)

cies (Table 2) and are well shown by Palmer (1962:plate opposite p. 184), Morrison & Gardner (1979:fig. 1), and Peterson (1980: 41). The San Salvador cormorants (Fig. 2) share with *P. auritus* essentially bare lores (orange-yellow in life) whereas in *P. brasilianus* the lores are sparsely feathered (Fig. 3). The feathered margin of the throat pouch is rounded in *P. auritus* and in the San Salvador cormorant, extending medially well beyond the level of the eye. In *P. brasilianus,* the margin is straight and scarcely reaches the level of the eye. The throat pouch and lower cheek are outlined in white in the breeding Olivaceous Cormorant, producing a characteristic "V" at the gape (Fig. 3), and white plumes and filoplumes decorate the head and neck. The eastern populations of *P. auritus* have black head tufts or crests during courtship, but, unlike the western subspecies, *P. a. cincinatus* and *P. a. albociliatus,* have no white on the head. Neither white feathers nor crests have as yet been noted in the field or in specimens of San Salvador birds. The dorsal feathers (notably the scapulars and upper wing coverts) are pointed in *P. brasilianus* but are more rounded in *P. auritus* and San Salvador birds (Fig. 4). In *P. brasilianus,* the tail is relatively longer in comparison with wing length and is more rounded than in *P. auritus* (Table 1).

Qualitative differences between the skeletons of *P. auritus* and *P. brasilianus* are slight. In the following cranial features, the population from San Salvador differs from *P. brasilianus* and agrees with *P. auritus*: (1) premaxilla in lateral or dorsoventral views less gracile, rising more steeply at the nasofrontal hinge; (2) posterior margins of palatines more truncated; (3) mandible in lateral view less gracile; (4) lacking the distinct ventral bowing in the region of the dentary/post-dentary articulation, with the ventral margin of the mandible thus appearing straighter. All of the major limb elements are noticeably more robust in San Salvador specimens than in *P. brasilianus.* This is especially true of the femur, in which the shaft is much heavier and the head markedly larger.

In all of these qualitative external and skeletal characters, the San Salvador cormorant agrees with *P. auritus,* of which it clearly represents an undescribed form differing in size.

Fig. 2. Subadult *Phalacrocorax auritus heuretus* on San Salvador, Bahama Islands, in 1981 shows pale lores and inconspicuous light feathering at posterior margin of throat pouch.

Most of the recently-collected specimens were prepared as complete skeletons and flat skins. Because size is the only character distinguishing the new subspecies, and skeletons provide many more measurements (and more accurate ones) than traditional study skins, a complete skeleton and flat skin has been designated holotype of the new subspecies.

Phalacrocorax auritus heuretus, new subspecies

Holotype.—Complete skeleton and flat skin USNM 556831 (original number SS-82-2), male (testes 5 × 14 mm), collected on Northwest Arm Lake, San Salvador Island, Bahamas, 19 Mar 1982, by Storrs L. Olson and Bertram N. Forbes.

Measurements of holotype.—Measurements (mm) are lengths of bones unless otherwise specified: mandible, 97.3; rostrum from nasofrontal hinge, 51.4; cranium from nasofrontal hinge, 52.5; width of sternum across first costal facet, 45.2; width of pelvis across antitrochanters, 32.8; greatest length of coracoid, 60.0; humerus, 125.5; ulna, 133.3; carpometacarpus, 57.7; femur, 49.2; tibiotarsus, 87.0; tarsometatarsus, 51.1. The following standard skin measurements were taken from the fresh specimen: culmen, 49.5; wing chord, 264; tail, 132. Weight: 1270 g.

Paratypes.—Seven complete skeletons and flat skins (3 males, 3 females, 1 unsexed): USNM 555523, 556828–556830, 556842–556844; and one unsexed incomplete postcranial skeleton, USNM 555585; a juvenile female postcranial skeleton with flat skin, USNM 556845; 12 study skins from San Salvador (2 adult males, 3 adult females, 1 unsexed adult, 3 immature males, 2 immature females, 1 unsexed immature):

Fig. 3. Adult *Phalacrocorax brasilianus* in breeding plumage, on Cat Island 1 December 1978 shows all-dark lores and the conspicuous white feathering on cheek and posterior margin of the throat pouch.

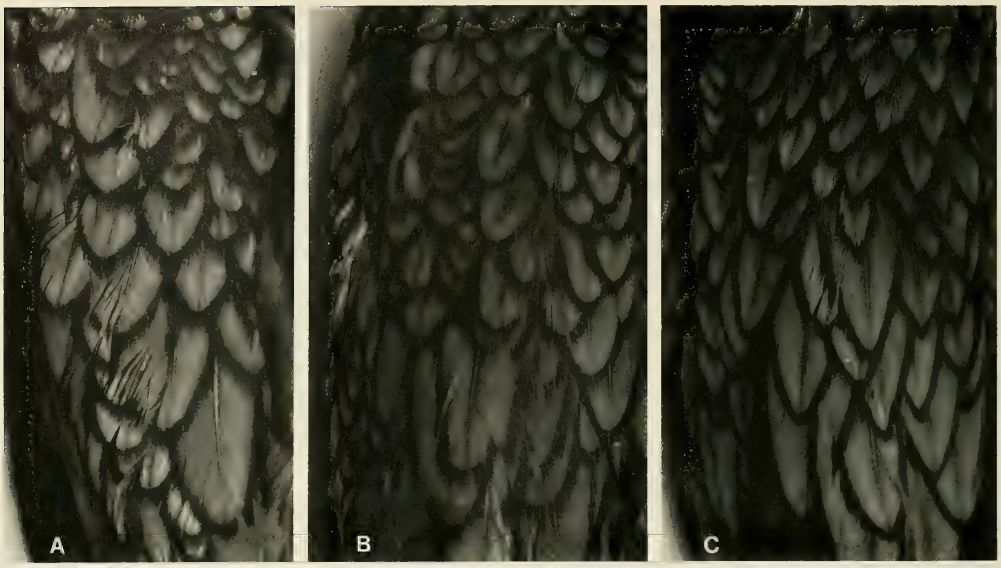


Fig. 4. Dorsal feathers of cormorants: *Phalacrocorax auritus floridanus* (*a*) and *P. a. heuretus* (*b*) are rounded at the tip while those of *P. brasilianus* (*c*) are more pointed.

CMNH 30908, FMNH 96432–96433, 96439–96440, SK 6653–6655 (=LSUMZ 141214–141216), USNM 108821–108822, 582413–582414. Three possibly mislabeled study skins from "Great" (=Grand) Bahama (1 adult male, 1 adult female, 1 immature male: FMNH 96426–96427, 96438) are tentatively referred to this subspecies (see below).

Other material examined.—Study skins: 8 *P. auritus floridanus,* Bahamas (4 males, 3 females, 1 unsexed): FMNH 7, SK (=LSUMZ) 1; 16 *P. a. floridanus,* Cuba (4 males, 11 females, 1 unsexed): AMNH 1, CMNH 7, FMNH 3, SK (=LSUMZ) 1, USNM 4; 53 *P. a. floridanus,* Florida (34 males, 17 females, 2 unsexed): AMNH 19, USNM 34; 6 *P. brasilianus mexicanus,* Cuba (2 males, 4 females): CMNH 2, SK (=LSUMZ) 3, USNM 1; 18 *P. b. mexicanus,* Texas (10 males, 8 females): AMNH 18. Skeletons: 11 *P. a. auritus*; 13 *P. a. flori-*

Table 2.—Comparison of characters in cormorants.

Character	*P. auritus*	*P. a. heuretus*	*P. brasilianus*
Lores	bare	bare	feathered
Gular pouch	rounded, extends behind eye	rounded, extends behind eye	cut off straight at level of eye
Gloss on head, neck	greenish	greenish	purplish
Head tufts or crests during courtship	curly, black	not recorded	wispy, white
White flecking on head and neck during courtship	absent in east coast populations	not recorded	present
White border to pouch during courtship	absent	not recorded	present
Shape of dorsal feathers	rounded	rounded	pointed
Tail length and shape	shorter, more squared	shorter, more squared	longer, more rounded

danus; and 16 *P. brasilianus mexicanus*: all in USNM, UF, and collection of P. Brodkorb.

Diagnosis.—Similar in morphology and coloration to *P. a. floridanus,* but markedly smaller, and consequently also smaller than any other population of *P. auritus,* with virtually no overlap in most measurements (Tables 1 & 3). Weights are also less than reported for other subspecies of *P. auritus* (Table 4). Weights and most external morphological measurements, except for those of tail and tail/wing ratios, are near those of *P. brasilianus mexicanus,* the smallest race of that species (Tables 1 & 4).

In skeletal measurements (Table 3), *P. a. heuretus* is much smaller than in any of the other forms of *P. auritus,* there being almost no overlap, even with the smallest subspecies, *P. a. floridanus.* Although generally more similar in size to *P. brasilianus,* the series of cormorant skeletons from San Salvador is clearly quite distinct mensurally from nominate *P. brasilianus* from Central America. The size of the cranium is virtually identical in these two series, yet the length of the rostrum and mandible averages greater in *P. brasilianus,* reflecting the relatively longer, more gracile bill in that species. In postcranial measurements, although there is some overlap, *P. a. heuretus* is consistently larger than *P. brasilianus.* The exception is in the carpometacarpus, the measurements for which are practically identical in these two populations. Given the larger size of *P. a. heuretus,* this may indicate a somewhat decreased flying ability associated with its more sedentary nature because when reductions in wing size take place, it is the distal elements that become reduced first (Livezey 1989).

Within both *P. auritus* (Palmer 1962) and *P. brasilianus* (P. C. Rasmussen in litt. 1990), high latitude populations are larger than those from nearer the Equator in conformity with Bergman's Rule. In the case of the San Salvador cormorant, however, latitude alone cannot account for the extreme size reduction because birds that breed at about the same latitude in southern Florida and further south on Cuba belong to the larger subspecies *P. a. floridanus.*

Range.—Known to breed only in the mangroves around some of the interior lakes of San Salvador in the eastern Bahama Islands, but possibly resident on other Bahaman islands (Cat Island, Buden 1987b). Subadult specimens of a male and a female (FMNH 96427, 96438, Table 1) that were collected by D. J. Sweeting, "one of Cory's hired guns" (David Willard in litt.), on "Great" (=Grand) Bahama Island on 23 and 7 October 1891, respectively, and an immature male collected there by Cory on 8 January 1879 (FMNH 96426, Table 1) are small and suggest either previous breeding of *P. a. heuretus* on that island (cf. Allen 1905), inter-island wandering or perhaps mislabelling. The last is suggested by the fact that Cory himself collected cormorants on San Salvador on 7 October 1891 and Sweeting collected specimens of other bird species on San Salvador on 3, 5, 12, 14, and 17 October 1891 (Willard in litt.). All Double-crested Cormorants collected on Cuba and the Isle of Pines belong to the larger subspecies, *P. a. floridanus* (Table 1).

Etymology.—The subspecific epithet is the latinized version of the Greek adjective, *euretós,* meaning "found," and refers both to our discovery of the cormorant's unsuspected specific relationship and to Columbus' discovery of the New World and possible landfall on San Salvador.

Discussion.—In the absence of adult specimens from the courting or early nesting periods, it is still unknown whether *P. a. heuretus* assumes breeding crests on the head. It is also uncertain whether *P. a. heuretus* is now restricted in its breeding to San Salvador. All but three of the specimens of *P. auritus* that we have examined from other Bahaman islands are significantly larger (Table 1) and are probably migrants of either the northern race, *P. a. auritus,* or the southeastern U.S. form, *P. a. floridanus.* In

Table 3.—Skeletal measurements (mm) of cormorants (*Phalacrocorax*).

Element		*n*	Range	Mean
Length of mandible	*P. brasilianus*	14	93.2–103.1	99.4
	P. a. heuretus	8	92.9–104.4	98.5
	P. a. floridanus	13	107.8–123.3	115.9
	P. a. auritus	11	109.1–127.1	118.3
Length of rostrum from nasofrontal hinge	*P. brasilianus*	14	47.0–56.6	53.7
	P. a. heuretus	7	48.7–56.3	51.7
	P. a. floridanus	13	58.8–68.6	63.6
	P. a. auritus	10	59.6–67.6	64.3
Length of cranium from nasofrontal hinge	*P. brasilianus*	14	48.7–53.9	51.6
	P. a. heuretus	7	48.9–54.6	51.8
	P. a. floridanus	13	55.0–61.1	58.0
	P. a. auritus	11	56.0–63.3	59.7
Width of sternum across first costal facet	*P. brasilianus*	15	39.0–46.3	42.9
	P. a. heuretus	7	44.1–48.8	47.0
	P. a. floridanus	13	49.2–56.7	52.6
	P. a. auritus	11	51.8–58.1	55.2
Width of pelvis across antitrochanters	*P. brasilianus*	16	28.5–31.5	30.1
	P. a. heuretus	6	30.0–33.5	32.1
	P. a. floridanus	13	32.1–36.1	34.2
	P. a. auritus	10	32.1–38.3	35.9
Greatest length of coracoid	*P. brasilianus*	15	55.5–62.6	59.9
	P. a. heuretus	9	57.7–62.5	60.4
	P. a. floridanus	13	62.1–71.1	67.0
	P. a. auritus	11	67.4–75.0	71.4
Length of humerus	*P. brasilianus*	15	110.2–125.1	118.6
	P. a. heuretus	9	120.7–131.4	126.6
	P. a. floridanus	13	131.2–151.5	139.4
	P. a. auritus	10	138.6–154.9	145.5
Length of ulna	*P. brasilianus*	15	117.8–134.9	126.4
	P. a. heuretus	9	126.1–138.2	133.8
	P. a. floridanus	13	133.7–161.0	147.2
	P. a. auritus	11	148.1–160.4	155.0
Length of carpometacarpus	*P. brasilianus*	15	55.4–63.5	58.3
	P. a. heuretus	9	54.7–61.0	58.4
	P. a. floridanus	12	62.8–71.6	66.7
	P. a. auritus	11	68.1–74.5	70.7
Length of femur	*P. brasilianus*	16	44.9–50.4	47.6
	P. a. heuretus	9	46.5–51.2	49.3
	P. a. floridanus	13	50.6–57.5	53.8
	P. a. auritus	11	54.2–61.7	57.6
Length of tibiotarsus	*P. brasilianus*	15	79.0–88.5	84.0
	P. a. heuretus	9	87.0–94.1	91.0
	P. a. floridanus	13	95.1–109.4	100.6
	P. a. auritus	11	100.8–110.8	105.5
Length of tarsometatarsus	*P. brasilianus*	14	47.6–53.3	49.9
	P. a. heuretus	9	51.0–54.2	52.7
	P. a. floridanus	13	56.4–64.8	59.9
	P. a. auritus	11	59.5–65.2	62.5

Table 4.—Weights of adult cormorants (*Phalacrocorax*). Those of *P. brasilianus mexicanus* (from New Mexico), *P. auritus heuretus* (San Salvador) and *P. a. albociliatus* (New Mexico) are from USNM specimens; those of *P. a. auritus* (Maine and Minnesota) and *P. a. floridanus* (Florida) are from Clapp et al. (1982).

Species	Males			Females		
	n	Range	Mean	*n*	Range	Mean
P. brasilianus	14	1150–1550	1393	8	1100–1450	1256
P. a. heuretus	1	1270		3	1036, 1126, 1175	1112
P. a. floridanus	6	1327–2079		5	1391–1665	
P. a. auritus	22	1986–2807		15	1750–2400	
P. a. albociliatus	16	2200–2750	2453	17	1750–2400	2056

recent years, *P. auritus* has not been found breeding elsewhere in the Bahama Islands (Bond 1980), but Allen (1905:119) reported small colonies of breeding Double-crested Cormorants observed during July 1904 on Abaco (10 pairs), Great Sal Cay (3 nests), and "Great" (=Grand) Bahama near Riding Point (nests only, birds "through breeding"). Cory (1880:198) collected two young that were out of the nest but were unable to fly, at Fresh Creek on Andros Island 18 January 1879 and Bonhote (1903) saw 8 to 10 pairs at empty nests at Wide Opening on the same island 31 January 1902. Bryant (1859) found Double-crested Cormorants "very abundant nesting in mangroves" in the Biminis. Young were "nearly fledged" 29 February 1859. The only specimen evidence for these records are two specimens that Allen collected 16 July 1904 on Great Sal Cay that are in the Museum of Comparative Zoology (MCZ 40186, 115000) and a male that Bonhote collected at Wide Opening, Andros, in the British Museum (BM 1924-4-10-180). All three of these specimens and five others from Andros and Grand Bahama have measurements that are within the range of *P. a. floridanus* (Table 1).

The Olivaceous Cormorant, on the other hand, is known to breed in the interior lakes of Great Inagua in the southernmost Bahamas (Buchheister 1966, Alexander Sprunt IV, National Audubon Society, Tavenier, Florida, 1984 in litt.; Buden 1987a, no specimens available) and on Cuba and the Isle of Pines (Garrido & Garcia Montaña 1975: 25; specimens examined). Sprunt (pers. comm., 1984) also reports seeing both *P. auritus* and *P. brasilianus* (some with white feathering) on Long Island, Bahamas, in late September 1984. Buden (1987b) reported that natives on Cat Island say that cormorants nest there. Of three skulls that he picked up on Cat Island in 1986 (specimens in MCZ), two were referable to *P. a. floridanus,* whereas the other was very small, like the birds of San Salvador. Miller, however, observed and photographed (Fig. 3) what appear to be prominent white borders on the throat pouches of cormorants breeding on Cat Island, and suspects that this population may also be referable to *P. brasilianus.* Some of the San Salvador cormorants in adult or near-adult plumage (FMNH 96438, USNM 555523, USNM 556844), however, retain a narrow fringe of pale buff or creamy immature feathers on the posterior edge of the gular pouch (Fig. 2), which might be confused in the field with the white nuptial feathers bordering the gular pouch in *P. brasilianus.* In adults of the latter species, however, the white is much brighter and is also present on the lower cheek, extending posteriorly from the angle of the gape to produce a marked "V" shape.

It is therefore highly desirable to obtain breeding specimens of cormorants from any other islands in the Bahamas, especially Long and Cat Islands and Great Inagua and

to obtain more observations and specimens of *P. a. heuretus* from San Salvador in courtship plumage.

Corroborating evidence of the specific identity of the San Salvador cormorant is potentially available from ectoparasites. Warren T. Ateyo (University of Georgia, 1983 in litt.) found on the San Salvador cormorant specimens a mite, *Michaelia watsoni,* a species known to parasitize *P. auritus,* but not *P. brasilianus.* Three kinds of feather lice (Mallophaga) inhabit the wings, body, and the inside of the throat pouch in cormorants, with different species of each being found on *P. auritus* and *P. brasilianus* (Emerson 1972:34–35). Unfortunately no lice have yet been found on specimens from San Salvador despite a vigorous search by K. C. Emerson. Neither did Miller find any in the gular pouches of four freshly collected birds and two live nestlings examined in 1981 and 1982.

On San Salvador, cormorants are restricted to the very extensive system of shallow interconnected inland lakes that dominate the physiography of the island (see Fig. 1, inset). These lakes are hypersaline and, although salinity may fluctuate with rainfall, evaporation rates greatly exceed precipitation (Rivers, 1985). Salinities measured in February 1976 and 1978 varied from 38‰ to 46‰ (Marshall 1982), whereas 14 determinations made in February and March 1985 were as high as 51‰ to 89‰. Analysis of fossil foraminifera and ostracodes revealed post-Pleistocene episodes of lower salinities (Bowman & Teeter 1982, Sanger & Teeter 1982), as also suggested by the former presence of an emydid turtle and a crocodilian on the island (Olson et al. 1990). Nevertheless, modern conditions present extremes of salt stress and only very euryhaline fishes can survive in these lakes. The ichthyofauna yet known consists of a poeciliid, *Gambusia manni,* an atherinid, *Atherinomorus stipes,* and killifishes, *Cyprinodon laciniatus* and a complex of several other species of *Cyprinodon.* Grant Gilmore (Harbor Branch Oceanographic Institute, Fort Pierce, Florida, in litt.) reports that none of the adult fish among more than 1000 specimens that he collected on San Salvador exceeded 50 mm in length.

Little is known of the food habits of cormorants on San Salvador except that they appear to feed nearly exclusively on *Cyprinodon* in the interior lakes. The few birds that are noted on the coastal beaches usually appear to be sick or injured. The stomachs of two birds collected by Olson in the Northwest Arm of Great Lake 19 March 1982 were crammed with small *Cyprinodon* (30–35 mm). He also found regurgitated remains of similar-sized *Cyprinodon* on sandbars in Great Lake from which cormorants had just been flushed. Owre (1967:131) reported the stomach contents of 11 of the larger *P. a. floridanus* taken in Florida, 9 in marine waters and 2 in fresh water. In contrast to the small size of the fish available to the San Salvador cormorants, the Florida prey remains, some headless, of 27 individuals of 7 species of fish ranged from 86 to 499 mm; the smallest intact fish was 136 mm. It seems possible that the diminutive subspecies *P. a. heuretus* is adapted to feeding on the small fishes in the inland lakes of San Salvador. Storer (1966) demonstrated a close relationship of size of prey and size of predators between sexes and among species of hawks of the genus *Accipiter,* but whether well-documented examples of small prey taken by small subspecies of piscivorous birds exist is less certain.

The San Salvador cormorant has been recorded as breeding during both winter and summer, but documentation of the latter is inadequate. Miller, on annual visits to San Salvador between 1973 and 1984, mainly in November, December, and January, found some asynchrony within and between colonies. Egg laying started in November and extended into early December; hatching began in early December; and most young were out of the nest by the end of January. From January to June 1976, he

recorded no breeding activity. Paulson (1966:2) also found "fully fledged young" on 31 December 1965. A juvenile female (USNM 556845), collected 1 February 1981, has wings and tail 80% grown, with the feather bases still ensheathed, and the head, throat, and hind neck entirely covered with down. Todd & Worthington (1911:404, 443) called Great Lake "the home of one or more rookeries of Mexican Cormorants," on the basis of Worthington's visit to an abandoned rookery 16 March 1909, where he found "dead young, about half grown, in various stages of decomposition." On the other hand, in mid-July, Riley (1905b:351) found "heavily incubated eggs, young sitting on the edge of nests and some already in the water with their parents, although they could not fly apparently." Breeding is also protracted in *P. a. floridanus* in Florida; egg dates extend from late December to early June (Bailey 1925:17; specimens in USNM collection).

Although no precise census has been made of the entire population of cormorants on San Salvador, it must certainly be small. Miller has found five breeding colonies of cormorants in red and black mangroves, *Rhizophora mangle* and *Avicennia nitida,* on San Salvador, four on Great Lake and one on a nearby pond. The colonies are widely scattered and not easily accessible. It is possible, but not highly likely, that one or two other small colonies exist, there being only three lakes that Miller did not check completely. In the 1981–1982 breeding season, the total nest count was 269. In 1982–1983, there were 256 nests, but 44 were probably unused older structures. The greatest number of individuals seen at one time was a raft of 110–130 birds recorded in April and May by Miller (1978:284), who also speaks of a small active colony east of Guana Cay on the south edge of Great Lake. Paulson (1966) found "more than 20 nests . . . on a large mangrove-covered island in a lake about 2.5 mi. SE Cockburn Town." He also observed a "moderate number . . . in flight over and fishing in Great Lake east of Cockburn Town" and speculated that there may be other colonies.

If 1981–1982 and 1982–1983 were average breeding seasons and if Miller's nest count for the latter season was complete, the total post-juvenile population of *P. a. heuretus* on the island was probably less than 600, with 424 breeding adults plus another 100 to 150 prebreeding yearlings and two-year-olds. Riley (1905b:351) found that young cormorants were "quite an item in the domestic economy of the islanders." Although the San Salvador cormorant is totally protected under the 1975 Bahamas Wild Birds Protection Act, in the experience of both Miller and Olson on San Salvador in recent years, cormorants are still shot for food and considered excellent table fare. Miller noted parts of butchered cormorants around Little Lake in early December 1977.

In view of its apparent uniqueness and the limited size of its population, the San Salvador cormorant ought to be a high conservation priority in the Bahama Islands. Continuing censuses of breeding pairs and counts or estimations of prebreeding populations of cormorants are needed, along with a search for breeding populations on other islands.

Acknowledgments

Olson's fieldwork on San Salvador in 1981 was sponsored by a grant from the National Geographic Society. Olson and Miller's work on San Salvador would not have been possible without the generous assistance of Dr. Donald Gerace, director of the College Center of the Finger Lakes Field Station, who facilitated every aspect of their residence and transportation on the island, was actively involved in obtaining additional specimens of cormorants for this study, and generously supplied references on the inland lakes of San Salvador. We are also grateful to Max Ferguson and Bertram N. Forbes for assistance in collecting specimens; to

Armand "Buck" Miller for measuring skeletons in the Smithsonian collections; to Jonathan Becker for supplying the measurements of *P. a. floridanus* in the collections of Pierce Brodkorb and the Florida State Museum; to Peter Colston, Raymond A. Paynter, Jr., and David Willard who reported on specimens in the British Museum (Natural History), Museum of Comparative Zoology (MCZ) and Field Museum of Natural History, respectively; and to the curators of the following collections who lent specimens for study or permitted access to their collections: American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CMNH), Florida Museum of Natural History (UF), Schwartz-Klinokowski Collection (SK, specimens are now in the Museum of Zoology of Louisiana State University, LSUMZ), and National Museum of Natural History (USNM). Pamela C. Rasmussen's careful and critical reading helped us improve the manuscript.

Literature Cited

Allen, G. M. 1905. Summer birds in the Bahamas.—The Auk 22:113–133.

American Ornithologists' Union. 1957. Check-list of North American birds, fifth edition. American Ornithololegists' Union, Baltimore, Maryland, 691 pp.

———. 1983. Check-list of North American birds, sixth edition. American Ornithologists' Union, [Washington, D.C.], 877 pp.

Bailey, H. H. 1925. The birds of Florida. Williams and Wilkins, Baltimore, Maryland, 146 pp.

Bond, J. 1956. Check-list of birds of the West Indies, fourth edition. Academy of Natural Sciences of Philadelphia, 214 pp.

———. 1980. Twenty-third supplement to the check-list of birds of the West Indies (1956). Academy of Natural Sciences of Philadelphia, 14 pp.

Bonhote, J. L. 1903. On a collection of birds from the northern islands of the Bahama group.—Ibis 8(3):273–315.

Bowman, P. A., & J. W. Teeter. 1982. The distribution of living and fossil foraminifera and their use in the interpretation of the post Pleistocene history of Little Lake, San Salvador Island, Bahamas.—College Center of the Finger Lakes Bahamian Field Station Occasional Papers 1982(2): 111 + 19 pp., appendix.

Browning, M. R. 1989. The correct name for the Olivaceous Cormorant, "Maiague" of Piso (1658).—Wilson Bulletin 101:101–106.

Bryant, H. 1859. A list of birds seen at the Bahamas, from Jan. 20, to May 14, 1859, with descriptions of new or little known species.—Proceedings of the Boston Society of Natural History 7:102–134.

Buchheister, C. W. 1966. The president reports.—Audubon Magazine 68:72–73.

Buden, D. W. 1987a. The birds of Cat Island, Bahamas.—Wilson Bulletin 99:579–600.

———. 1987b. The birds of the southern Bahamas. British Ornithologists' Union Checklist, number 8. British Ornithologists' Union, London, 119 pp.

Clapp, R. B., R. C. Banks, D. Morgan-Jacobs, & W. A. Hoffman. 1982. Marine birds of the southeastern United States and Gulf of Mexico. Part 1, Gaviiformes through Pelecaniformes. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C., 637 pp.

Cory, C. B. 1880. Birds of the Bahama Islands. C. B. Cory, Boston Massachusetts, 250 pp.

———. 1892a. A list of birds taken on Maraguana, Watling's Island and Inagua, Bahamas, during July, August, September and October, 1891.—The Auk 9:48–49.

———. 1892b. Catalogue of West Indian birds. C. B. Cory, Boston, Massachusetts, 163 pp.

Dorst, J., & J.-L. Mougin. 1979. Order Pelecaniformes. Pp. 155–193 *in* E. Mayr & G. W. Cottrell, eds., Check-list of birds of the world, volume 1, second edition. Museum of Comparative Zoology, Cambridge, Massachusetts.

Emerson, K. C. 1972. Checklist of the Mallophaga of North America (north of Mexico), part 4, bird host list. Dugway, Utah, Desert Test Center, 119 pp.

Garrido, O. H., & F. Garcia Montaña. 1975. Catálogo de las aves de Cuba. Academia de Ciencias de Cuba, Habana, Cuba, 149 pp.

Hellmayr, C. E., & B. Conover. 1948. Catalogue of birds of the Americas and adjacent islands in Field Museum of Natural History, part 1, number 2. Publications of the Field Museum of Natural History, Zoological Series, volume 13, vii + 434 pp.

Livezey, B. C. 1989. Flightlessness in grebes (Aves, Podicipedidae): its independent evolution in three genera.—Evolution 43:29–54.

Marshall, H. G. 1982. Phytoplankton composition from two saline lakes in San Salvador, Bahamas.—Bulletin of Marine Science 32:351–353.

Miller, J. R. 1978. Notes on birds of San Salvador Island (Watlings), the Bahamas.—The Auk 95: 281–287.

Morrison, M. L., & D. Gardner. 1979. The cormo-

rants of Texas.—Bulletin of the Texas Ornithological Society 12:35–36.

Olson, S. L., G. K. Pregill, & W. B. Hilgartner. 1990. Studies on fossil and extant vertebrates from San Salvador (Watling's) Island, Bahamas.—Smithsonian Contributions to Zoology 508:1–15.

Owre, O. T. 1967. Adaptations for locomotion and feeding in the Anhinga and the Double-crested Cormorant.—Ornitholological Monographs 6, 138 pp.

Palmer, R. S., ed. 1962. Handbook of North American birds, volume 1. Yale University Press, New Haven, Connecticut, 565 pp.

Paulson, D. R. 1966. New records of birds from the Bahama Islands.—Notulae Naturae, number 394, 15 pp.

Peterson, R. T. 1980. A field guide to the birds, fourth edition. Houghton Mifflin, Boston, Massachusetts, 384 pp.

Richardson, P. L., & R. A. Goldsmith. 1987. The Columbus landfall: voyage track corrected for winds and currents.—Oceanus 30:2–10.

Ridgway, R. 1891. List of birds collected on the Bahama Islands by the naturalists of the Fish Commission Steamer *Albatross*.—The Auk 8:333–339.

Riley, J. H. 1905a. Birds. Pp. 347–368 *in* G. B. Shattuck, ed., The Bahama Islands. Geographical Society of Baltimore.

———. 1905b. List of birds collected or observed during the Bahama expedition of the Geographical Society of Baltimore.—The Auk 22:349–360.

Rivers, W. G. 1985. Halophytes of the hypersaline lakes of San Salvador, Bahamas. Pp. 87–89 *in* R. R. Smith, ed., Proceedings of the First Symposium on the Botany of the Bahamas. College Center of the Finger Lakes Bahamian Field Station, San Salvador, Bahamas.

Sanger, D. B., & J. W. Teeter. 1982. The distribution of living and fossil ostracoda and their use in the interpretation of the post-Pleistocene history of Little Lake, San Salvador Island, Bahamas. College Center of the Finger Lakes Bahamian Field Station Occasional Papers 1982(1):111 + 19 pp., appendix.

Storer, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters.—The Auk 83:423–436.

Todd, W. E. C., & Worthington, W. W. 1911. A contribution to the ornithology of the Bahama Islands.—Annals of the Carnegie Museum 7: 388–464.

(GEW) 4323 Cathedral Avenue, NW, Washington, D.C. 20016; (SLO) Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (JRM) R. D. 1, Box 1152, Maryland, New York 12116.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 370–386

SYSTEMATICS OF THE COATIS, GENUS *NASUA* (MAMMALIA: PROCYONIDAE)

Denise M. Decker

Abstract.—Systematics of the genus *Nasua* was examined using both qualitative and quantitative techniques. Principal component analysis was used to assess morphologic variation among the species of *Nasua.* Mann-Whitney *U* tests were used to determine whether there were any differences among the three taxa in any of the quantitative features measured and to determine whether the Cozumel coati was significantly smaller than *N. narica* of the Yucatan peninsula (including the Yucatan, Campeche, and Quintana Roo departments). Morphological features were examined to determine whether there were any qualitative features that could distinguish between any of the species of *Nasua.* Principal component analysis showed that *N. nelsoni* was not distinctly smaller in body size when compared to a series of mainland coatis. Mann-Whitney *U* tests revealed significant differences between *N. nasua* and *N. narica* ($P < 0.01$) in most quantitative features measured. Significant differences ($P < 0.05$) were found between Yucatan *N. narica* and *N. nelsoni* for 27 of the 32 quantitative features measured; however, when *N. nelsoni* was compared to a geographically representative sample of mainland *N. narica,* only 16 of the 32 features were significant ($P < 0.05$). Eight qualitative features, including features of the anterior alveolar foramen, nasal bones, postorbital process of the jugal bone, mesopterygoid region of the palate, m2 entoconid, baculum, nose color, and hair at the nape of the neck were found to separate *N. nasua* from *N. narica* and *N. nelsoni.* Differences in the quantitative analyses between *N. nasua* and *N. narica* and between *N. nelsoni* and *N. narica* are differences commonly seen at the subspecific level and are not considered of sufficient nature to recognize any of the taxa as distinct species based on these quantitative features. The qualitative features were found useful in separating *N. nasua* from *N. narica.* No qualitative features were found to separate *N. nelsoni* from *N. narica.* Based on results of this study, *N. nelsoni* should be considered conspecific with *N. narica.* Therefore, only two species of *Nasua* (*N. nasua* and *N. narica*) are recognized.

Historically, species-level systematics of the coatis (genus *Nasua*) has been influenced by the large range of color and size variation, much of which has been attributed to differences in sex and age (Burt & Hooper 1941, Hershkovitz 1951). Individual variation is such that Allen (1906) described different pelage colorations, previously used as subspecific designations, from a series of specimens collected at the same time from a single locality. Individuals with different pelage coloration also have been reported in the same litter (Allen 1879). In northwestern Mexico, Burt & Hooper (1941) found that the only well-defined geographic trend is in coloration, with specimens becoming progressively darker from north to south. This variation has led to a number

of incorrect identifications, and the taxonomy of *Nasua* remains uncertain (Appendix 1).

Two (Corbet & Hill 1986, Honacki et al. 1982) or three (Ewer 1973) species of coatis are recognized currently, *Nasua narica* (white-nosed coati), *Nasua nasua* (brown-nosed coati), and *Nasua nelsoni* (Cozumel Island coati). Authors who have recognized only two species have lumped North American *N. narica* with South American *N. nasua* and considered the insular *N. nelsoni* as a distinct species. *Nasua nelsoni* generally has been accepted as a distinct species based on the original description by Merriam (1901) and its validity has not been questioned subsequently. *Nasua nasua* and *N. narica* were described originally by Linnaeus (1766), who based the description of *N. nasua* on the "coati" of Marcgrave (1648) and the "coati-mondie a queue annelee" of Brisson (1756) and that of *N. narica* on the "Coati brun" of Buffon (1760). *Nasua nelsoni* was distinguished from *N. narica* primarily on the basis of its smaller size (Merriam 1901). No diagnostic qualitative features have been reported by Merriam (1901) or by later authors. Jones & Lawlor (1965) retained *N. nelsoni* as a species, believing that it was smaller than *N. narica yucatanica* of the adjacent mainland.

Nasua narica has been considered conspecific with *N. nasua* by several authors (Hall 1981, Honacki et al. 1982, Corbet & Hill 1986, Nowak & Paradiso 1986) despite the lack of any published data to support this conclusion. Those authors cite (directly or indirectly) a passage in Cabrera (1960: 245) concerning the color morphs of South American coatis: "Al parecer, todos los *Nasua* sudamericanos constituyen una sola especie con dos fases cromaticas, una parda y otra roja, y en algunos casos con marcada tendencia al melanismo . . . ." However, Cabrera was not referring to the comparison between North and South American coatis but rather to the two color phases of South American coatis (brown phase, *Nasua nasua* Linnaeus, 1766 and red phase, *Nasua rufa* E. Geoffroy Sainte-Hilaire, 1803), each previously thought to represent separate South American species. Cabrera (1960) considered all South American forms as one species (*Nasua nasua*) and was not concerned with the North American form, *N. narica*. A detailed analysis of the *N. narica-nasua* problem has not been attempted.

Because original descriptions were based on a small number of highly variable features, the taxonomic status of *Nasua* is unclear and in need of additional investigation (Eisenberg 1989). For this study, I tested the hypothesis that *N. nasua, N. narica,* and *N. nelsoni* can be distinguished on either quantitative or qualitative morphological features. This was tested in two ways: (1) by examining characters that were used in the original type descriptions and in subsequent published descriptions; (2) by examining variation in additional characters (characters not used in previous studies).

Methods

For the quantitative analysis of morphological variation, 32 measurements were recorded from 111 male and 116 female specimens (Appendix 2) with digital calipers and recorded to the nearest 0.01 mm. Measurements employed are listed in Table 1 and described in Decker (1990). Specimens (including nine holotypes) were selected from a wide geographic range (Appendix 2 and Fig. 1) to account for the great amount of variation exhibited in the genus *Nasua*. Preliminary analyses indicated sexual dimorphism in 22 of 32 skull characters for each described species, with males being consistently larger than females. Males and females were analyzed separately in each analysis. Pair-wise comparisons were made between *N. nasua* and *N. narica* and between *N. nelsoni* and *N. narica* using a Mann-Whitney *U* test to determine whether there were any differences in measured characters. A Mann-Whitney *U* test was

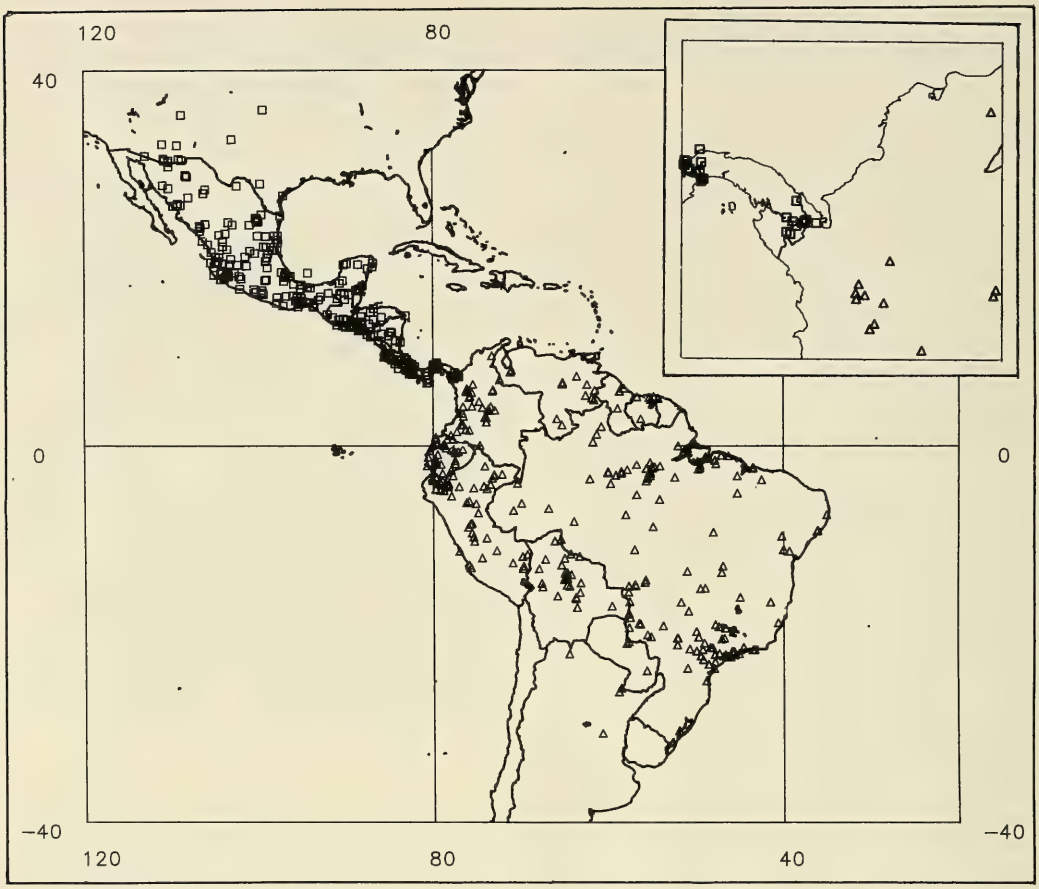


Fig. 1. The geographic range of specimens examined in this study. {△} = *N. nasua*; {□} = *N. narica*. Inset shows closeup of Panama/Colombia and the allopatric distribution (see text for discussion).

performed between *N. nelsoni* and *N. narica* of the Yucatan (including the Yucatan, Campeche, and Quintana Roo departments) to test Jones & Lawlor's (1965) assumption that the Cozumel Island coati is smaller than the adjacent mainland coati (*N. narica yucatanica*). Principal component analysis was used to assess morphologic variation among taxa. Because of the range of variation exhibited by individuals from the same locality, each specimen was treated as an operational taxonomic unit (OTU).

Qualitative features that have been used previously to distinguish among taxa were taken initially from the type description and from discussions in subsequent literature. Other morphological features were added based on observations of 684 specimens (Appendix 2). Characters were scored as to presence or absence within each taxon.

Results and Discussion

A Mann-Whitney *U* test revealed significant differences between *N. nasua* and *N. narica* ($P < 0.01$) for most characters measured (Table 1). Infraorbital foramen height was the only feature that did not differ significantly in either sex. The distance between paroccipital process and mastoid process was not significantly different in males. Premaxillary length, rostrum length, palate length, zygomatic breadth, and cranium

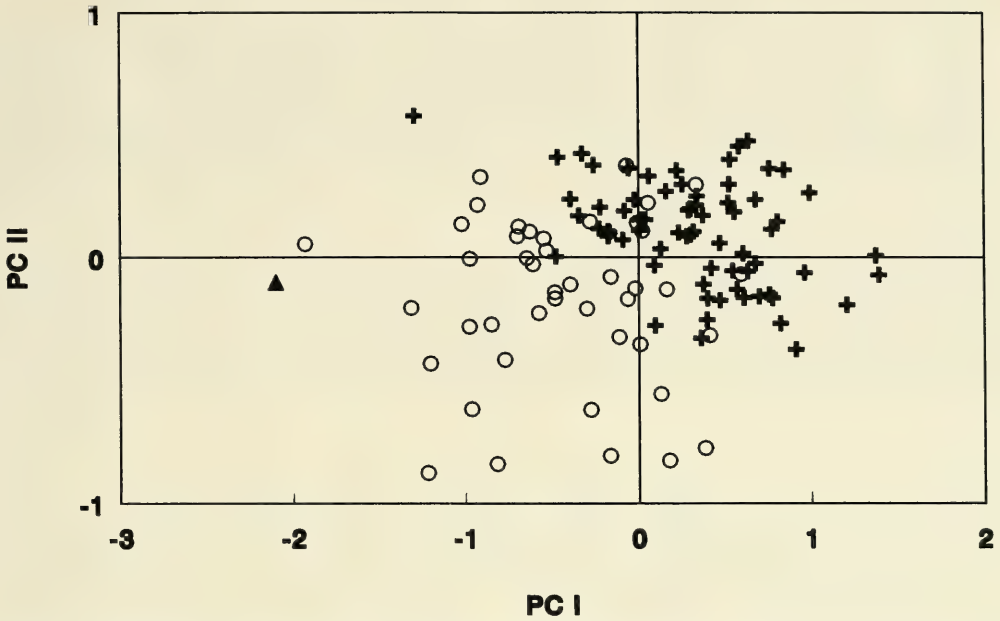


Fig. 2. Scattergram showing the results of principal component analysis of *N. nasua* {+}, *N. narica nelsoni* {▲} and *N. narica* {O}.

width are the characters best able to distinguish between *N. nasua* and *N. narica*; however, because there is so much overlap even in these features, these skull measurements would not be useful in identifying a single individual. Slightly less significant differences ($P < 0.05$) were found in 16 of the 32 characters measured between *N. narica* and *N. nelsoni* for both males and females. Five of the six specimens of *N. nelsoni* used in this study were collected from the same locality at the same time; therefore, it is possible that most specimens from the sample of *N. nelsoni* are from one family unit. Because the Cozumel Island coatis were collected from one local population, this sample is probably not a good representation of the variation of the Cozumel coati. There probably are several local populations of mainland coatis that fall well within the range of variation of the Cozumel coati. For example, I have found a series of coatis in Estado Nuevo Leon, Mexico that do not differ in size from the Cozumel coati. Because of the lack of adequate sampling on the island, the variation is probably much greater than represented. Despite this fact, a clear separation could not be found between *N. narica* and *N. nelsoni*. The three taxa were not easily distinguishable using principal component analysis (Fig. 2). *Nasua nasua* and *N. nelsoni* were both well within the range of variation of *N. narica*. Twenty-four of the 32 characters loaded high on principal component I (PCI), accounting for 86% of the variation. PCI has been interpreted as representing size (Kennedy & Schnell 1978, Neff & Marcus 1980, Best 1985). These results indicated that there was no apparent size difference in the quantitative features among *N. nasua, N. narica,* and island forms of *N. nelsoni*.

Jones & Lawlor's (1965) observation that the Cozumel coati is slightly smaller than the adjacent mainland coati, *N. narica yucatanica* was supported (Table 2). However, when the Cozumel coati is compared to a widely distributed and well sampled population of mainland coatis, the differences are not as clear (Table 1). Of the 32 char-

Table 1.—The mean, standard error, sample size (n) and range for skull measurements of the genus *Nasua*. '*' denotes a significant difference of *N. nasua* or *nelsoni* from *N. narica* at the 0.05 level of significance. '**' denotes a significant difference at the 0.01 level as revealed by a Mann-Whitney U test.

Character	*N. nasua*(♂♂)	*N. nasua*(♀♀)	*N. narica*(♂♂)	*N. narica*(♀♀)	*N. nelsoni*(♂♂)	*N. nelsoni*(♀♀)
CBL	117.98 1.063**	108.53 0.968**	125.50 0.796	119.36 0.560	98.17 1.050*	97.15 3.73*
	$n = 36$	$n = 26$	$n = 65$	$n = 79$	$n = 2$	$n = 2$
	(104.04–129.30)	(99.10–121.83)	(99.91–136.06)	(109.14–135.70)	(97.12–99.22)	(93.42–100.88)
ZYB	66.42 1.056**	56.76 0.775**	70.83 0.871	62.22 0.432	58.11 1.550*	49.39 0.495*
	$n = 36$	$n = 28$	$n = 69$	$n = 83$	$n = 2$	$n = 2$
	(54.07–78.21)	(51.76–67.03)	(50.90–82.12)	(55.17–77.44)	(56.56–59.66)	(48.89–49.88)
PPL	85.74 0.920**	78.33 0.883**	92.01 0.787	87.74 0.581	71.27	69.47 0.395*
	$n = 27$	$n = 19$	$n = 47$	$n = 55$	$n = 1$	$n = 2$
	(78.05–93.48)	(71.96–90.32)	(71.79–101.18)	(78.65–100.34)	—	(69.07–69.86)
ROS	21.49 0.42188**	19.24 1.131**	23.45 0.282	20.84 0.480	19.01 1.310*	15.82 0.375*
	$n = 38$	$n = 29$	$n = 69$	$n = 84$	$n = 3$	$n = 2$
	(17.04–27.55)	(14.97–28.91)	(17.35–27.36)	(16.71–38.74)	(16.44–20.74)	(15.44–16.19)
IFH	4.84 0.087	4.78 0.103	4.84 0.073	4.66 0.062	5.06 0.510	4.63 0.435
	$n = 38$	$n = 30$	$n = 69$	$n = 84$	$n = 3$	$n = 2$
	(3.89–5.98)	(3.64–6.34)	(3.44–6.66)	(3.38–6.63)	(4.19–5.06)	(4.19–5.06)
PAL	72.90 0.678**	67.44 0.730**	78.94 0.541	75.19 0.415	60.18 2.170*	58.75 0.960*
	$n = 35$	$n = 24$	$n = 63$	$n = 75$	$n = 2$	$n = 2$
	(65.07–81.68)	(61.16–76.91)	(62.50–86.48)	(68.54–86.73)	(58.01–62.35)	(57.79–59.71)
POP	32.63 0.563**	29.11 0.493**	36.44 0.442	34.15 0.292	28.85 1.015*	26.34
	$n = 34$	$n = 28$	$n = 64$	$n = 77$	$n = 2$	$n = 1$
	(26.12–40.46)	(24.68–33.29)	(26.27–44.56)	(34.15–40.84)	(27.83–29.86)	—
MAX	46.39 0.374**	44.24 0.423**	49.27 0.335	47.60 0.209	39.87 1.476*	37.77 0.350*
	$n = 36$	$n = 28$	$n = 65$	$n = 82$	$n = 3$	$n = 2$
	(43.00–51.00)	(40.00–49.00)	(40.00–55.00)	(43.00–52.00)	(37.00–42.00)	(37.00–38.00)
PMX	48.48 0.400**	45.86 0.439**	51.36 0.330	49.51 0.210	41.52 1.372*	39.46 0.350*
	$n = 35$	$n = 29$	$n = 67$	$n = 82$	$n = 3$	$n = 2$
	(44.44–53.49)	(41.15–52.24)	(41.34–57.27)	(45.43–53.97)	(38.83–43.33)	(39.11–39.81)
WFM	15.25 1.762**	13.34 0.166**	14.21 0.088	13.92 0.074	11.94 0.175*	11.95
	$n = 34$	$n = 26$	$n = 62$	$n = 72$	$n = 2$	$n = 1$
	(11.97–17.15)	(10.82–14.55)	(12.32–16.14)	(12.43–15.31)	(11.76–12.11)	—
MAS	45.10 1.243**	40.50 1.094**	47.66 0.358	44.74 0.241	40.09 2.165*	35.78 0.795*
	$n = 37$	$n = 28$	$n = 68$	$n = 80$	$n = 2$	$n = 2$
	(34.47–73.15)	(23.40–48.16)	(37.54–53.92)	(40.41–50.88)	(37.92–42.25)	(34.98–36.57)

Table 1.—Continued.

Character	*N. nasua*(♂♂)	*N. nasua*(♀♀)	*N. narica*(♂♂)	*N. narica*(♀♀)	*N. nelsoni*(♂♂)	*N. nelsoni*(♀♀)
PCB	23.42 0.359**	24.88 0.367**	27.41 0.316	29.68 0.213	23.35 0.415	25.24
	$n = 38$	$n = 30$	$n = 67$	$n = 76$	$n = 2$	$n = 1$
	(19.02–29.83)	(20.31–29.29)	(20.89–31.57)	(26.14–34.04)	(22.93–23.76)	—
ABL	14.18 0.177**	13.71 0.213**	16.26 0.118	15.71 0.101	13.23 0.250*	11.68 0.425*
	$n = 38$	$n = 29$	$n = 68$	$n = 81$	$n = 2$	$n = 2$
	(12.37–16.85)	(11.98–16.41)	(12.08–18.46)	(12.21–17.76)	(12.98–13.48)	(11.25–12.10)
ABW	14.67 0.218*	13.94 0.223*	15.25 0.123	14.54 0.112	11.49 0.000*	10.38 0.270*
	$n = 38$	$n = 29$	$n = 69$	$n = 81$	$n = 2$	$n = 2$
	(12.11–17.46)	(11.90–16.44)	(11.86–17.55)	(12.31–16.86)	(11.49–11.49)	(10.11–10.65)
ABH	6.59 0.125**	6.29 0.179**	7.81 0.125	7.70 0.109	5.51 0.580*	5.95
	$n = 38$	$n = 27$	$n = 63$	$n = 74$	$n = 2$	$n = 1$
	(4.77–8.13)	(3.68–7.84)	(6.07–9.90)	(5.68–10.01)	(4.93–6.09)	—
INB	25.87 0.317**	24.12 0.272**	28.18 0.384	26.98 0.227	17.94 3.170*	20.68
	$n = 37$	$n = 30$	$n = 64$	$n = 75$	$n = 2$	$n = 1$
	(22.00–29.00)	(21.00–27.00)	(18.00–34.00)	(22.00–32.00)	(15.00–21.00)	—
ROL	56.10 0.476**	51.80 0.470**	58.83 0.407	55.58 0.474	45.98 1.127**	44.14
	$n = 38$	$n = 30$	$n = 66$	$n = 79$	$n = 3$	$n = 1$
	(50.33–60.93)	(45.74–58.30)	(45.09–64.18)	(25.66–63.58)	(44.54–48.20)	—
MEW	15.60 0.195**	15.08 0.221**	17.22 0.128	17.26 0.116	13.95 0.415*	14.93
	$n = 38$	$n = 28$	$n = 63$	$n = 75$	$n = 2$	$n = 1$
	(12.75–17.58)	(13.48–18.12)	(15.35–19.94)	(14.38–20.25)	(13.53–14.36)	—
MEL	18.11 0.320**	16.19 0.345**	21.56 0.243	20.81 0.809	14.44 0.085*	13.48
	$n = 37$	$n = 24$	$n = 60$	$n = 70$	$n = 2$	$n = 1$
	(14.45–22.06)	(12.47–19.84)	(16.16–25.93)	(15.74–74.75)	(14.35–14.52)	—
PAR	13.48 0.210	11.82 0.213*	13.76 0.162	12.66 0.130	10.88 0.760*	9.57 0.435*
	$n = 38$	$n = 29$	$n = 67$	$n = 82$	$n = 2$	$n = 2$
	(10.34–16.36)	(9.12–13.91)	(8.20–16.21)	(7.41–15.20)	(10.12–11.64)	(9.13–10.00)
COR	26.03 0.419**	23.22 0.495**	29.95 0.253	28.33 0.179	22.13 0.718*	22.62
	$n = 38$	$n = 30$	$n = 66$	$n = 79$	$n = 3$	$n = 1$
	(21.13–33.81)	(18.86–30.19)	(23.62–34.55)	(23.28–32.83)	(21.20–23.54)	—
FRO	32.94 0.418**	30.46 0.604**	35.32 0.363	32.73 0.253	26.82 2.960*	25.13
	$n = 38$	$n = 30$	$n = 64$	$n = 76$	$n = 2$	$n = 1$
	(27.83–38.59)	(24.94–43.66)	(23.87–40.74)	(28.11–41.36)	(23.86–29.78)	—

Table 1.—Continued.

Character	*N. nasua*(♂♂)	*N. nasua*(♀♀)	*N. narica*(♂♂)	*N. narica*(♀♀)	*N. nelsoni*(♂♂)	*N. nelsoni*(♀♀)
WCR	43.84 0.238**	41.70 1.314**	45.51 0.185	44.68 0.134	38.49 0.530*	37.95
	$n = 38$	$n = 29$	$n = 65$	$n = 73$	$n = 2$	$n = 1$
	(40.60–46.84)	(25.32–45.46)	(41.62–49.38)	(42.27–47.56)	(37.96–39.02)	—
PL3	5.49 0.081**	5.41 0.117*	6.06 0.049	6.33 0.384	4.36 0.082**	4.55
	$n = 34$	$n = 29$	$n = 63$	$n = 78$	$n = 3$	$n = 1$
	(4.49–6.17)	(3.57–6.68)	(5.23–7.01)	(4.98–8.75)	(4.20–4.46)	—
PB3	3.59 0.080**	3.70 0.161**	4.10 0.050	4.10 0.037	3.27 0.090**	3.30
	$n = 34$	$n = 29$	$n = 63$	$n = 78$	$n = 3$	$n = 1$
	(2.89–4.70)	(2.82–6.91)	(3.16–5.26)	(3.29–4.87)	(3.11–3.42)	—
PL4	6.95 0.087**	6.72 0.093**	7.46 0.064	7.52 0.049	5.45 0.119*	6.10 0.235*
	$n = 37$	$n = 29$	$n = 67$	$n = 84$	$n = 3$	$n = 2$
	(5.41–8.11)	(5.89–7.94)	(6.02–8.73)	(6.58–8.64)	(5.25–5.66)	(5.86–6.33)
PB4	6.88 0.096**	6.65 0.104**	7.69 0.071	7.61 0.062	5.52 0.131*	5.77 0.400*
	$n = 37$	$n = 29$	$n = 67$	$n = 84$	$n = 3$	$n = 2$
	(5.26–7.85)	(5.65–7.94)	(5.45–8.93)	(6.11–8.94)	(5.28–5.73)	(5.37–6.17)
ML1	7.27 0.099**	6.94 0.097**	7.78 0.060	7.59 0.048	6.00 0.090*	6.10 0.260*
	$n = 36$	$n = 28$	$n = 68$	$n = 83$	$n = 3$	$n = 2$
	(5.97–8.33)	(6.09–8.17)	(5.96–8.94)	(6.48–8.63)	(5.89–6.18)	(5.84–6.36)
MB1	6.56 0.092**	6.41 0.097*	7.73 0.052	7.62 0.052	6.08 0.171*	6.65 0.205*
	$n = 36$	$n = 28$	$n = 68$	$n = 83$	$n = 3$	$n = 2$
	(5.35–7.82)	(5.50–7.55)	(6.84–8.74)	(7.62–8.71)	(5.77–6.36)	(6.44–6.85)
ML2	6.33 0.121**	6.18 0.154**	6.94 0.082	6.90 0.069	4.87 0.225*	4.36 0.050*
	$n = 37$	$n = 29$	$n = 66$	$n = 84$	$n = 3$	$n = 2$
	(4.82–7.71)	(4.29–7.48)	(5.15–8.25)	(5.67–8.40)	(4.49–5.27)	(4.31–4.41)
MB2	6.63 0.108**	6.51 0.143**	7.84 0.056	7.75 0.053	5.93 0.261*	6.21 0.005*
	$n = 37$	$n = 28$	$n = 65$	$n = 84$	$n = 3$	$n = 2$
	(5.19–7.90)	(4.95–8.12)	(6.86–8.79)	(6.86–9.16)	(5.42–6.27)	(6.20–6.21)
BAS	32.65 0.625*	28.47 0.809*	34.50 0.476	32.17 0.319	25.92	—
	$n = 12$	$n = 7$	$n = 19$	$n = 24$	$n = 1$	—
	(28.33–36.06)	(26.43–32.12)	(30.64–37.67)	(30.02–35.64)	—	—

acters examined, the 16 that are significant ($P < 0.01$) are related to the length of the skull and the size of the dentition. Comparisons with the skull of *N. narica* reveal an increase in the length of the skull of the Cozumel coati, while the width of the braincase remains the same. Additionally, the dentition of the Cozumel coati is also smaller in both length and width. The lengthening of the skull and the reduction of the dentition is probably associated with a shift in the diet of the Cozumel coati.

In the original description, Merriam (1901) compared Cozumel Island coatis (holotype specimen plus two males and four females) to a single specimen of *N. narica* from the Yucatan peninsula. The description of the holotype emphasized a smaller skull, zygomatic arch, auditory bullae, and dentition. Results of this study show that the variation of these features in *N. nelsoni* is within the range of variation of *N. narica* (Table 1). Based on the few specimens of mainland coatis that Merriam (1901) had to compare with the Cozumel coati, the features he emphasized as being the most important discriminators are significantly different from that of *N. narica* in this study. However, when the Cozumel coati is compared to a representative sample of *N. narica,* the differences are not as great.

Characters that were found significantly different in this study between *N. nelsoni* and *N. narica* have been shown to be of value in geographic variation studies and in delineating subspecies (e.g., Kortlucke 1973, Kennedy & Lindsay 1984). The differences among the subspecies of *N. narica* are greater than those between *N. narica* and *N. nelsoni.* Therefore, if one were to recognize *N. nelsoni* as a distinct species based on the few differences revealed at the 0.05 level of significance, it would be necessary to split the recognized subspecies of *N. narica* (see Hall 1981) into many species as well. Therefore, differences between *N. nelsoni* and *N. narica* are not of sufficient nature to warrant specific recognition.

Table 2.—Results of Mann-Whitney *U* test between Yucatan *N. narica* and Cozumel Island *N. nelsoni. n* = sample size (*N. narica*/*N. nelsoni*).

Character	*n*	*df*	*Z*	*P*
CBL	10/5	14	−2.33	0.020
ZYB	10/5	14	−1.71	0.086
PPL	11/4	13	−2.61	0.009
ROS	11/6	15	−1.81	0.070
IFH	11/6	15	−0.60	0.547
PAL	9/5	13	−3.00	0.003
POP	8/4	11	−1.36	0.174
MAX	11/6	14	−3.22	0.001
PMX	11/6	15	−3.02	0.003
WFM	8/3	10	−2.45	0.014
MAS	10/5	14	−2.45	0.014
PCB	10/4	13	−2.40	0.016
ABL	11/5	14	−3.12	0.002
ABW	11/5	14	−2.89	0.004
ABH	9/3	10	−2.50	0.013
INB	8/3	10	−2.45	0.014
ROL	9/4	11	−2.78	0.006
MEW	8/3	10	−2.45	0.014
MEL	7/3	9	−2.39	0.017
PAR	11/5	14	−2.44	0.015
COR	9/4	11	−2.78	0.006
FRO	8/3	10	−2.25	0.025
WCR	8/3	10	−2.45	0.014
PL3	9/4	10	−2.78	0.006
PB3	9/4	10	−2.78	0.006
PL4	11/6	14	−3.32	0.001
PB4	11/6	14	−2.82	0.005
ML1	11/6	14	−3.02	0.003
MB1	11/6	14	−2.31	0.021
ML2	11/6	14	−3.22	0.001
MB2	11/6	14	−2.81	0.005
BAS	3/1	2	−1.34	0.180

There is no question that the Cozumel coatis are typically small, but the variation overlaps with the mainland coati for most characters measured. This tendency to be slightly smaller may be related to island dwarfism. Factors that may cause body size to increase or decrease in insular populations include metabolic considerations, resource availability, predation, and competition (Case 1978, Heaney 1978) and probably have different roles in different species. Lawlor (1982) proposed that mammals which specialize on a diet of particulate nature decrease in size on islands, whereas generalists that feed on nonparticu-

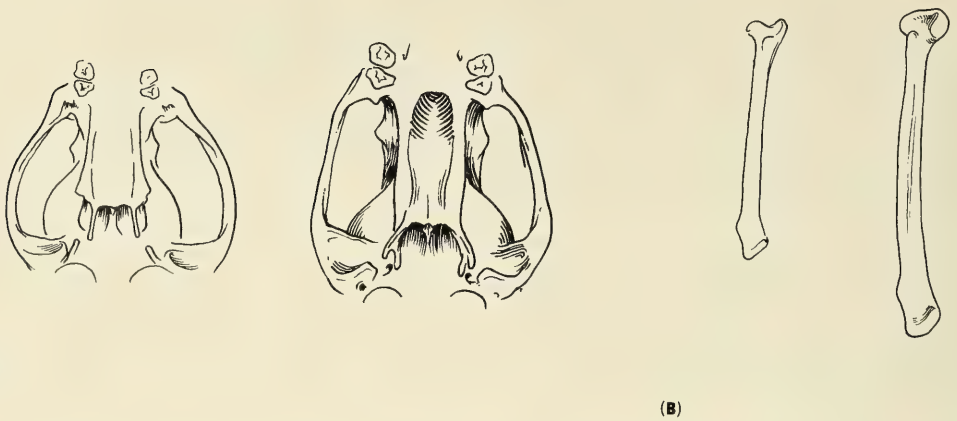


Fig. 3. A ventral view of *N. nasua* (left) and *N. narica* (right) demonstrating a feature of the palate; (b) Bacula of *N. narica* (left) and *N. nasua* (right).

late foods increase in size. Although the mainland coatis are generalists, the Cozumel coati may not be. This study suggests that the Cozumel coati is specializing on smaller prey items, but additional study of its ecology and behavior is necessary.

Size does not appear to discriminate populations. *Nasua nelsoni* cannot be clearly differentiated from *N. narica* based on the original size-related features used in the type description or on subsequent measured variables if a representative sample of *N. narica* from a wide geographic range is used in the comparison.

Of 100 qualitative features examined, eight separate *N. nasua* from *N. narica* and none separate *N. nelsoni* from *N. narica* (Table 3). Of the eight, five are features of the skull and dentition, one of the postcranial skeleton, and two of the pelage. Of the five skull features, the most easily discernible is a feature of the palate (Fig. 3a) first recognized by Alston (1879). The mesopterygoid region of the palate is flat in *N. nasua,* whereas in *N. narica* (and *N. nelsoni*) it is depressed along the midline resulting in a relatively small distance between the presphenoid and palate (ca. 2.20 mm in *N. narica* versus 4.70 mm in *N. nasua*). In *N. narica,* the vomer extends beyond and attaches to the posterior portion of the palate and can be easily seen in ventral view. The distance between the presphenoid and palate of *N. nasua* is much greater than in *N. narica* (and *N. nelsoni*) and the vomer does not reach the posterior edge.

Additional skull features that distinguish *N. nasua* from *N. narica* (and *N. nelsoni*) include features of the rostrum. In *N. nasua,* the anterior alveolar foramen (as used by Wahlert 1974, Cooper & Schiller 1975, Shoshani 1986) is situated anterior to the infraorbital canal, whereas in *N. narica* (and *N. nelsoni*), it is medial to the infraorbital canal and cannot be seen in lateral view. The alveolar foramen serves as a passageway for the anterior superior alveolar nerve along with a small artery and vein (Shoshani, pers. comm.). The sides of the nasal bones are parallel in *N. narica* (and *N. nelsoni*) so that the posterior width is about equal to the anterior width. In *N. nasua,* the nasal bones converge posteriorly so that the most posterior width is less than the most anterior width. The postorbital process of the jugal bone is present in *N. nasua* and absent in *N. narica* (and *N. nelsoni*). In the dentition, the entoconid of the second lower molar is present and very distinctive in *N. narica* (and *N. nelsoni*), causing the molar to

have a well defined talonid. The entoconid is absent in *N. nasua* and the talonid is indistinct.

In the postcranial skeleton, only one feature of the baculum was found that discriminated among OTUs. The distal tip of the baculum (Fig. 3b) of *N. narica* (and *N. nelsoni*) is distinctly bilobed with a vestigial third lobe on the ventral surface. The baculum of *N. nasua* is spatulate dorsally with a prominent central lobe on the ventral surface. Pocock (1921) noted that the bacula of *N. nasua* and *N. narica* differ significantly in length and commented that this difference may be diagnostic. I examined seven bacula and there seems to be a size difference. However, the utility of size as a diagnostic character remains uncertain, as the variability in baculum size over the whole geographic range has not been examined.

Differences among the many described forms of coatis have usually centered on external pelage. The color of the nose adjacent to the rhinarium distinguishes *N. narica* (and *N. nelsoni*) from *N. nasua* and was used commonly by early authors (Linnaeus 1766, Allen 1879, Alston 1879). *Nasua narica* (and *N. nelsoni*) have a white rhinarial patch and in *N. nasua* it varies from gray to brown (i.e., absent), but is never white. My observations confirm those of A. Gardner (pers. comm.) who recognized that the hair at the nape of the neck is reversed in *N. nasua,* but not in *N. narica* (and *N. nelsoni*).

The eight characters of the skull, postcranial, and skin, discussed above, are diagnostic and justify recognition of *N. narica* as a species distinct from *N. nasua.* Nose color and presence or absence of the postorbital process do not vary in any part of the species' range. Other skull features, such as the position of the rostral foramen and concavity of the palate, were found to vary slightly at the extreme ends (in Mexico for *N. narica* and in southern Brazil for *N. nasua*) of the species' range, however, where the ranges are contiguous, these features are always discrete. For identification, the following key should be used together with locality.

Table 3.—Qualitative features used to separate species of the genus *Nasua.* The plus (+) denotes the presence of the character and the dash (−) denotes the absence of the character. NAS = *Nasua nasua*; NAR = *N. narica*; and NEL = *N. nelsoni.*

Character	NAS	NAR	NEL
Anterior alveolar foramen medial to infraorbital foramen	+	−	−
Nasal bones converge posteriorly	+	−	−
Mesopterygoid depression	−	+	+
Preorbital process	+	−	−
m2 entoconid	+	−	−
Baculum bilobate	−	+	+
Muzzle white	−	+	+
Nape hair reversed	+	−	−

Key to Species of *Nasua*

1. Palate flat (not concave along midline); nasal bones converging posteriorly; anterior alveolar foramen anterior to infraorbital canal; postorbital process (of jugal) present; M2 entoconid absent; spatulate baculum; brown muzzle ..... *N. nasua*
2. Palate depressed along midline; nasal bones near parallel; anterior alveolar foramen medial to infraorbital canal; postorbital process (of jugal) absent; M2 entoconid absent; baculum not spatulate; white muzzle .. *N. narica* (including *N. n. nelsoni*)

The geographic range of *N. narica* extends from southern Arizona and southwestern New Mexico southward throughout Mexico and Central America with three specimens reported from northern Colombia, Gulf of Uraba (FMNH 69599, 69600, 69601). The range of *N. nasua* extends throughout most of northern South America to northern Argentina and northern Uruguay (Fig. 1). The

apparent lack of parapatry of the two species in northern Colombia may be a collecting artifact.

Conclusion

Eight qualitative features were found to separate *Nasua nasua* from *N. narica* (including *N. n. nelsoni*). No qualitative features were found to distinguish *N. n. nelsoni* from *N. narica,* and *Nasua n. nelsoni* is not distinctly smaller in body size when compared to a geographically representative sample of mainland coatis. Consequently, I propose that *N. nelsoni* be considered conspecific with *N. narica* and recognize only two species, *Nasua nasua* and *N. narica.*

Acknowledgments

I would like to thank M. L. Beck, M. Carleton, A. Gardner, G. D. Johnson, M. L. Kennedy, R. D. Owen, F. Weckerly, and W. C. Wozencraft for critically reviewing earlier drafts of this manuscript. W. C. Wozencraft prepared Fig. 1 and Fig. 2, and T. Foster prepared Fig. 3. Funds for this study were provided by the Department of Biology, Memphis State University; The Vertebrate Museum, Shippensburg University; Department of Zoology, University of Tennessee; the Office of the Assistant Secretary for Research, Smithsonian Institution; and National Museum of Natural History, Smithsonian Institution. The following institutions kindly offered the use of their specimens and facilities: American Museum of Natural History; Field Museum of Natural History; Florida State Museum, University of Florida; Louisiana State University, Museum of Zoology; Museum of Comparative Zoology, Harvard University; Museum of Natural History, University of Kansas; Museum of Vertebrate Zoology, University of California; National Museum of Natural History; Philadelphia Academy of Natural Sciences; The Museum, Michigan State University.

Literature Cited

Allen, J. A. 1879. On the coatis (genus *Nasua,* Storr).—Bulletin of the United States Geological and Geographical Survey 5:153–174.

———. 1904. New Mammals from Venezuela and Colombia.—Bulletin of the American Museum of Natural History 20:29–80.

———. 1906. Mammals from the states of Sinaloa and Jalisco, Mexico, collected by F. H. Batty during 1904 and 1905.—Bulletin of the American Museum of Natural History 22:191–262.

———. 1916. List of mammals collected for the American Museum in Ecuador by William B. Richardson, 1912–1913.—Bulletin of the American Museum of Natural History 35:113–125.

Alston, E. R. 1879. Biologica Centrali-Americana. Mammalia. R. H. Porter, London, 220 pp.

Avila-Pires, F. D. de. 1965. The type specimens of Brazilian mammals collected by Prince Maximilian zu Wied.—American Museum Novitates 2209:1–21.

Best, T. L. 1985. Variation in kangaroo rats (genus *Dipodomys*) of the heermanni group in Baja California, Mexico.—Journal of Mammalogy 59: 160–175.

Brisson, M. J. 1756. Le regnum animale in classes IX distributum, sive synopsis methodica sistensgeneralem animalium distributionem in classes IX, and duarum primarum classium, quadrupedum scilicet and cetaceorum, particularem divisionem in ordines, sectiones, genera and species. C. J. B. Bauche, Paris, 384 pp.

Buffon, G. L. L. 1760 Buffon's natural history of man, the globe and of quadrupeds, with additions from Cuvier, Lacepede, and other eminent naturalists. World Publishing House, New York.

Burt, W. H., & E. T. Hooper. 1941. Notes on mammals from Sonora and Chihuahua, Mexico.—Occassional Papers, Museum of Zoology, University of Michigan 430:1–7.

Cabrera, A. 1956. Una neuva forma del Genero *Nasua.*—Neotropica 2:1–4.

———. 1958–1961. Catalogo de los mamiferos de America del sur. Buenos Aires, 732 pp.

Case, T. J. 1978. A general explanation for insular body size trends in terrestrial vertebrates.—Ecology 59:1–18.

Cooper, G., & A. L. Schiller. 1975. Anatomy of the guinea pig. Harvard University Press, Cambridge, 417 pp.

Corbet, G. B., & J. E. Hill. 1986 A world list of mammalian species. Second ed. British Museum of Natural History, London, 226 pp.

Cuvier, G. 1798. Tableau elementaire de l'histoire naturelle des animaux. Baudouin, Paris, 710 pp.

Daudin, F. M. 1799 [1802]. *In* Buffon, Histoire naturelle, generale et particuliere: Quadrupeds. par Didot. F. Dufart, Paris, volume 14.

Decker, D. M. 1990. Systematics of the coatis (genus *Nasua*). Unpublished M.S. thesis, Memphis State University, Memphis, Tennessee, 88 pp.

Desmarest, A. G. 1820. Mammalogie, ou description des especes de mammiferes, vol. I. Premiere partie, contenant les ordes des bimanes, des quadrumunes et des carnassiers. Encyclopedie Methodique, V. Agasse, Paris, 556 pp.

Dougenik, J. A., & D. E. Sheehan. 1975. SYMAP user's reference manual. Fifth ed., Lab. Computer Graphics and Spatial Analysis, Harvard University, Cambridge.

Eisenberg, J. F. 1989. Mammals of the Neotropics. University of Chicago Press, Chicago, 449 pp.

Erxleben, J. C. P. 1777. Systema regni animalis per classes, ordines, genera, species, varietates cum synonymia et histoire animalium. Classis I. Mammalia. Lipsiae, Impensis Weygandianis, 636 pp.

Ewer, R. F. 1973. The carnivores. Cornell University Press, Ithaca, 494 pp.

Fischer, J. B. 1829. Synopsis mammalium. Stuttgart, 752 pp.

Fischer Von Waldheim, G. 1814. Zoognosia tabulis synopticus illustrata. Moscow, volume 2, 605 pp.

Geoffroy Sainte-Hilaire, E. 1803. Catalogue des Mammiferes du Museum National d'Histoire Naturelle. Paris, 272 pp.

Gmelin, J. F. 1788. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis synonymis locis. O. E. Beiv, Lipsiae, 13th edition, 3 volumes.

Goldman, E. A. 1932. A new coati from Nicaragua.—Journal of the Washington Academy of Sciences 22:312–313.

———. 1942. Notes on the coatis of the Mexican mainland.—Proceedings of the Biological Society of Washington 55:79–82.

Gray, J. E. 1843. List of the specimens of Mammalia in the collection of the British Museum. British Museum (Natural History), London, 216 pp.

———. 1866. Notice of a new species of *Nasua*.—Proceedings of the Zoological Society of London 1866:169–170.

———. 1869. Catologue of carnivorous, pachydermatous, and edentate Mammalia in the British Museum. British Museum (Natural History), London, 398 pp.

Hagmann, K. 1908. Rostrattsreformen. Det hvilande grundlagsforslaget, lagen om val till Riksdagen Samt lagarna ang. andringar i kommunalforfattningarna med inledning forklaringar och register; Valhandbek. P. A. Norstedt, Stockholm, 229 pp.

Hall, E. R., & K. R. Kelson. 1959. The mammals of North America. The Ronald Press Company, New York, 2 volumes.

———. 1981. Mammals of North America. John Wiley and Sons, New York, 2 volumes.

Handley, C. O. 1966. Checklist of mammals of Panama. Pp. 753–793 *in* R. L. Wenzel & V. J. Tipton, eds., Ectoparasites of Panama. Chicago Field Museum of Natural History, 861 pp.

Heaney, L. R. 1978. Island area and body size of insular mammals: Evidence from the tri-colored squirrel (*Callosciurus prevosti*) of southwest Asia.—Evolution 32:39–44.

Hershkovitz, P. 1951. Mammals from British Honduras, Mexico, Jamaica and Haiti.—Fieldiana, Zoology 31:547–569.

Honacki, J. H., K. E. Kinman & J. W. Koeppl, (eds). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc. and The Association of Systematic Collections, Lawrence, Kansas, 694 pp.

Ihering, H. 1911. Os mammiferos do Brazil Meriodinal.—Revista Museo Paulista 8:147–272.

Illiger, J. K. W. 1815. Uberlick der Saugthiere nach ihrer vertheilung Uber die Welt-theile. Abhandlungen. Koniglich-preussische Akademie der Wissenschaften, Physikalische Klassa, 1804–1811:39–159.

Jones, J. K., Jr., & T. E. Lawlor. 1965. Mammals from Isla Cozumel, Mexico, with description of a new species of harvest mouse.—University of Kansas Publications 16:409–419.

Kennedy, M. L., & S. L. Lindsay. 1984. Morphologic variation in the raccoon, *Procyon lotor*, and its relationship to genic and environmental variation.—Journal of Mammalogy 65:195–205.

———, & G. D. Schnell. 1978. Geographic variation and sexual dimorphism in Ord's kangaroo rat, *Dipodomys ordii*.—Journal of Mammalogy 59: 45–59.

Kortlucke, S. M. 1973. Morphological variation in the kinkajou, *Potos flavus* (Mammalia: Procyonidae), in Middle America. Occassional Papers of the Museum of Natural History, University of Kansas, No. 17, 36 pp.

Lacepede, B. G. E. 1799. Discours d'ouverture et de Cloture du cours d'histoire naturelle des animaux vertebres et a sang rouge. Paris, chez Plassan, Imprimeur Libraire, 57 pp.

Lawlor, T. E. 1982. The evolution of body size in mammals: evidence from insular populations in Mexico.—American Naturalist 119:54–72.

Lesson, R. P. 1842. Moeurs, instinct et singularities de la vie des animaux mammiferes par R. P. Lesson. Paris, 294 pp.

Liais, E. 1872. Climats, geologie, faune et geographie botanique du Bresil. Garnier Freres, Paris, 640 pp.

Linnaeus, C. 1766. Systema nature per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentilii synonymis, locis. Twelfth edition, Larentius Salvii, Holmiae, 3 volumes.

Lonnberg, E. 1921. A second contribution to the mammalogy of Ecuador with some remarks on Caenolestes.—Arkiv for Zoologica 14:1–104.

Marcgrave, J. 1648. Historia Natural Do Brasil. Museu Paulista Comemorativa do Fundacao da Imprensa Oficial do Estado de Sao Paulo, Brazil, 293 pp + CIV.

Merriam, C. H. 1901. Six new mammals from Cozumel Island, Yucatan.—Proceedings of the Biological Society of Washington 14:99–104.

———. 1902. Five new mammals from Mexico.—Proceedings of the Biological Society of Washington 15:67–69.

Neff, N. A., & L. F. Marcus. 1980. A survey of multivariate methods for systematics. Privately published, New York, 243 pp.

Nowak, R. M., & J. L. Paradiso. 1986. Walker's mammals of the world; 2 vols, fourth ed. John Hopkins University Press, Baltimore.

Olfers, I. von. 1818. Bemerkungen zu Illiger's Ueberblick der Saugthiere nach ihrer Vertheilung uber die Welttheile, rucksichtlich der Sudamericanischen Arten (Species). Abhandlung X of Wilhelm Ludwig Eschwege's Journal von Brasilien, 15:192–223.

Pocock, R. I. 1921. The external characters and classification of the Procyonidae.—Proceedings of the Zoological Society of London 28:389–422.

Rohlf, F. J., J. Kishpaugh, & D. Kirk. 1982. Numerical taxonomy system of multivariate statistical programs. New York State University, Stony Brook, (various pagings).

Schinz, H. R. 1821. *In* Cuvier, Das Thierreich eingetheilt nach dem Bau der thiere als Grundlage ihere Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier, Staatsrath von Franzreich und bestandiger Secretar der Academie der Wissenschaften U.S.M.: Aus dem Franzosischen fren ubersett und mit vielen Zusatzen versehen von H.R Schinz. Stuttgart und Tubingen, volume 1.

———. 1844–1845. Systematisches Vereichniss aller bis jetzt bekannten Saugethiere; oder, Synopsis mammalium nach dem Cuvier' schen system. Solothurn, Jent und Gassmann, 2 vols.

Shoshani, J. 1986. On the phylogenetic relationships among Paenungulata and within Elephantidae as demonstrated by molecular and osteological evidence. Unpublished Ph.D. dissertation, Wayne State Unversity, Detroit, 700 pp.

Storr, G. C. C. 1780. Prodromus methodi mammalium. Tubingae. Litteris Reissimis, 43 pp.

Tate, G. H. H. 1939. The mammals of the Guiana region.—Bulletin of the American Museum of Natural History 76:151–229.

Thomas, O. 1901. New neotropical mammals, with a note on the species of Reithrodon.—Annals and Magazine of Natural History, Ser. 7, 8:246–255.

———. 1912. Two new species of *Nasua*.—Annals and Magazine of Natural History, Ser. 8, 10: 228–230.

———. 1914. New *Nasua, Lutra,* and *Proechimys* from South America.—Annals and Magazine of Natural History, Ser. 8,14:57–61.

———. 1927. The Godman-Thomas expedition to Peru—on mammals collected by Mr. R. W. Hendee in the province of San Martin, N. Peru, mostly at Yurac Yacu.—Annals and Magazine of Natural History, Ser. 9, 19:361–368.

Tschudi, J. J. von. 1844–1846. Untersuchungen uber die Fauna Peruana. St. Gallen, volume 1 (various pagings).

Vieira, C. 1945. Sobre uma colecao de Mamiferos de Mato Grosso.—Arquivos de Zoologia do Estado de Sao Paulo 4:395–430.

Wahlert, J. 1974. The cranial foramina of protrogomorphous rodents: an anatomical and phylogenetic study.—Bulletin of the Museum of Comparative Zoology 146:363–411.

Weinland, D. F. 1860. Was zu einem "ganzen" Thiere gehort und wie man vielleicht Tropenthiere gefunder erhatten konnte.—Zoologische Garten 11:185–200.

Wied-Neuwied, Maximillian, A. P., prinz von. 1826. Beitrage zur naturgeschichte von Brasilien, von Maximillian, prinzen zu Wied. Landes-Industrie-Comptoirs, Weimar, volume 2.

Winge, H. 1895. Jordfundne og nulevende rovdye (Carnivora) fra Lagoa Santa, Minas Geraes, Brasilien. Bianco Lunos Kgl, hof-bogtrykkeri, 103 pp.

Yates, T. L., W. R. Barber, & D. M. Armstrong. 1987. Survey of North American collections of Recent mammals.—Journal of Mammalogy, supplement 68:1–76.

Biology Department, Memphis State University, Memphis, Tennessee 38152. Present address: Graduate Program in Ethology, M313 Walters Life Science, University of Tennessee, Knoxville, Tennessee 37996.

Appendix 1.—Synonymys of the genus *Nasua*.

Viverra Linnaeus, 1766:64 (part).
Ursus G. Cuvier, 1798:113 (part).
Nasua Storr, 1780:35; type species *Viverra nasua* Linnaeus, 1766, by absolute tautonymy.
Coati Lacepede, 1799:7; type species *Coati nasua* Lacepede, 1799 (=*Viverra nasua* Linnaeus, 1766) by monotypy.
Cuati Liais, 1872:427; incorrect subsequent spelling of *Coati* Lacepede, 1799.

Nasua narica (Linnaeus, 1766)
White-nosed coati

[*Viverra*] *narica* Linnaeus, 1766:64; type locality "America." Subsequently restricted to "Veracruz, Mexico" by Allen (1879) and further restricted to Achotal, Isthmus of Tehuantepec, Veracruz by Hershkovitz (1951:560).
[*Viverra*] *vulpecula* Erxleben, 1777:490 (part); type locality "in Mexico."
Ursus narica: G. Cuvier, 1798:113; name combination.
Coati narica: Daudin, 1799:154; name combination.
Nasua narica: E. Geoffroy St.-Hilaire, 1803:86; name combination.
Nasua nasica Winge, 1895:35; unjustified emendation of *Viverra narica* Linnaeus, 1766. Alston (1879:74) also insisted that Linnaeus intended the name to be nasica, meaning "with a long or pointed nose," but mispelled it.
Nasua solitaria mexicana Weinland, 1860:191; type locality "mexico."
Nasua nelsoni Merriam, 1901:100; type locality "Cozumel Island, Yucatan," Mexico.
Nasua narica molaris Merriam, 1902:68; type locality "Manzanillo, Colima, Mexico."
Nasua narica bullata Allen, 1904:48; type locality "Pozo Azul, Pirris Province, Costa Rica."
Nasua narica panamensis Allen, 1904:51; type locality "Boqueron, Chiriqui," Panama.
Nasua narica yucatanica Allen, 1904:52; type locality "Chichenitza, Yucatan," Mexico.
Nasua narica pallida Allen, 1904:53; type locality "Sierra Nevada (vicinity of Guadalupe y Calva), Chihuahua, Mexico."
Nasua narica richmondi Goldman, 1932:312; type locality "Escondido River, 50 miles above Bluefields, Nicaragua."
Nasua narica tamaulipensis Goldman, 1942:80; type locality "Cerro de la Silla, near Monterrey, Nuevo Leon, Mexico (altitude 2,600 feet)."
Nasua narica isthmicus Goldman, 1942:81; type locality "Santa Efigenia, an hacienda about eight miles northwest of Tapanatepec, southeastern Oaxaca, Mexico (altitude 1,200 feet)."

Appendix 1.—Continued.

Nasua nasua (Linnaeus, 1766)
Brown-nosed coati

[*Viverra*] *nasua* Linnaeus, 1766:64; type locality "America."
[*Nasua*] *nasua* Storr, 1780: 35; first use of current name combination, generic description.
[*Viverra*] *quasje* Gmelin, 1788:87 (part); type locality "Surinami."
Ursus nasua: G. Cuvier, 1798:113; name combination.
Nasua rufa E. Geoffroy St.-Hilaire, 1803:85; type locality "L'Amerique."
Nasua quasje: E. Geoffroy St.-Hilaire, 1803:85; name combination.
Nasua pusillus E. Geoffroy St.-Hilaire, 1803:87; type locality "L'Amerique meridionale," restricted to French Guiana by Desmarest (1820:15).
[*Nasua*] *rufa* Fischer von Waldheim, 1814:175; type locality "in regionibus calidis Americae." Synonym and homonym of *N. rufa,* E. Geoffroy St.-Hilaire, 1803.
[*Nasua*] *fusca* Fischer von Waldheim, 1814:176; type locality "in regionibus calidis Americae."
N [*asua*]. *obfuscata* Olfers, 1818: 227; type locality "Brasilien."
N [*asua*]. *mondie* Olfers, 1818:227; type locality "Brasilien."
Nasua rufa Desmarest, 1820:170; type locality "L'Amerique meridionale"; synonym and homonym of *N. rufa* E. Geoffroy St.-Hilaire, 1803.
Nasua fusca Desmarest, 1820:170; type locality "L'Amerique meridionale"; synonym and homonym of *N. fusca* Fischer, 1814.
Nasua sociabilis Schinz, 1821:199; type locality "in Brasilien."
Nasua solitaria Schinz, 1821:199; type locality "in Brasilien." Restricted to "Morro d'Arara, Rio Mucuri, state of Bahia, Brazil," by Avila-Pires (1965).
N[*asua*]. *socialis* Weid-Neuwied, 1826:283; type locality restricted to "Morro d'Arara, Rio Mucuri, state of Bahia, Brazil," by Avila-Pires (1965).
[*Nasua socialis*] *Rufa*: Fischer, 1829:148; name combination.
[*Nasua socialis*] *Fusca*: Fischer, 1829:148; name combination.
[*Nasua socialis*] *aurea* Lesson, 1842:77; type locality not mentioned, based on "coati brun" of F. Cuvier, Pl. 1.
Nasua monticola Schinz, 1844:310; type locality "Peru."
Nasua nasuta Tschudi, 1845:99; incorrect subsequent spelling of *N. nasua* Linnaeus, 1766.
Nasua rufina Tschudi, 1845:99; incorrect subsequent spelling of *N. rufa* Desmarest, 1820.
Nasua leucorhynchus Tschudi, 1845:100; type locality

Appendix 1.—Continued.

not known. "It is often brought by travellers from the interior of Brazil, but there is apparently good reason for questioning the correctness of the locality" (Allen, 1879).

Nasua vittata Tschudi, 1845:100; type locality "Innern von Guyana."

N[asua]. montana Tschudi, 1845:102; type locality Umanpuqio, "Cejaregion," Peru.

Nasua dorsalis Gray, 1866:169; type locality "South America."

Nasua leucorphya Gray, 1869:36; incorrect subsequent spelling of *Nasua leucorhynchus* Tschudi, 1845.

Nasua quichua Thomas, 1901:248; type locality "Jima, Central region of Cordilleras, Province of Azuay, Ecuador."

Nasua phaeocephala Allen, 1904:334; type locality "Suapure, Caura district, Venezuela."

Nasua socialis mexiana Hagmann, 1908:12; type locality "Insel Mexiana," Para, Brazil.

Nasua narica juruana Ihering, 1911:239; type locality "Rio Jurua," Brazil.

Nasua candace Thomas, 1912:228; type locality "Medellin, Antioquia, Colombia."

Nasua manium Thomas, 1912:229; type locality "Balzar Mts., N.W. of Guayaquil, western Ecuador."

Nasua quichua jivaro Thomas, 1914:58; type locality "Gualaquiza, Oriente [Morrona-Santiago] Ecuador; alt. 2500 feet.

Nasua judex Thomas, 1914:57; type locality "Bogota, Colombia."

Nasua nasua manium: Allen, 1916:121; name combination.

Nasua nasua candace: Allen, 1916:221; name combination.

Nasua nasua quichua: Allen, 1916:122; name combination.

Nasua nasua soderstromii Lonnberg, 1921:98; type locality "near Baeza, road to Napo, Ecuador."

Nasua nasua soederstroemmii Lonnberg, 1921:98; (Cabrera, 1958:246); mandatory change in spelling of *N. n. soderstrommii* Lonnberg, 1921.

Nasua gualeae Lonnberg, 1921:30; type locality "Gualea, Ecuador."

Appendix 1.—Continued.

Nasua henselii Lonnberg, 1921:102; type locality "Sta Catharina, S. Brazil."

Nasua henselii cinerascens Lonnberg, 1921:103; type locality "Rio de Oro, a small tributary to Rio Paraguay, near mouth of Rio Bermejo, Chaco Austral, Argentina."

Nasua nasua mephisto Thomas, 1927:367; type locality "Yurac Yacu, Peru, 2500'."

Nasua candace dichromatica Tate, 1939:200; type locality "plateau of Mt. Auyantepui, S. Venezuela, at approximately 6000 feet."

[*Nasua*] *juruana*: Tate, 1939:200; name combination.

[*Nasua*] *jivaro*: Tate, 1939:200; name combination.

Nasua nasua aricana Vieira, 1945:404; type locality "Faz. Arica, Rio Arica, sul de Cuiaba," Mato Grosso, Brazil.

Nasua nasua mexianae Vieira, 1945:410; name combination.

Nasua nasua solitaria: Vieira, 1945:410; name combination.

Nasua nasua boliviensis Cabrera, 1956:2; type locality "provincia de Chapare, departamento de Cochabamba, Bolivia, a 1.500 m de altitud."

Nasua nasua cinerascens: Cabrera, 1958:246; name combination.

Nasua nasua dorsalis: Cabrera, 1958:246; name combination.

Nasua nasua montana: Cabrera, 1958:247; name combination.

Nasua nasua quichua: Cabrera, 1958:247; name combination.

Nasua nasua vittata: Cabrera, 1958:248; name combination.

Nasua nasua molaris: Hall and Kelson, 1959:976; name combination.

Nasua nasua yucatanica: Hall and Kelson, 1959:976; name combination.

Remarks: The following species names have been incorrectly applied and are invalid: *monde, squash, spadicea, quasje, minor, canina* (Illiger, 1815:109); *nocturna* (Wied, 1826:298); *olivacea* (Gray, 1843: 195).

Appendix 2.—Specimens Examined.—Specimens denoted with "**" were used in both the quantitative and qualitative analyses. Specimens denoted with "*" were used only in the qualitative analyses. Locality data are given in Decker (1990). Museum acronyms for museums in the United States follow Yates et al. (1987), other acronyms are as follows: BMNH = British Museum of Natural History.

N. nasua.—AMNH 333*, 15091*, 15296*, 16051*, 16304*, 16717*, 16776*, 17557*, 24420*, 21626*, 26400*, 26522*, 28498*, 29256*, 30203*, 31167*, 32357*, 33040**, 33042**, 33043**, 33044**, 33247*, 34348*, 33899**, 36461*, 36480**, 36585*, 36586*, 36587*, 36588*, 36964*, 36974*, 38801*, 38802*, 38803*, 39989*, 40832*, 41943*, 42449*, 46516*, 46517*, 46518*, 46521*, 61437*, 61438*, 61603*, 61872*, 62854*, 64043*, 67100*, 67705*, 67714*, 68313*, 68314*, 71361**, 71841*, 73764*, 74459*, 76036*, 76642*, 77694*, 78594*, 81487*, 83294*, 88202*, 88204*, 91788*, 91792*, 93668*, 94152*, 95096*, 95293*, 95297*, 96296*, 96298*, 96300*, 98493*, 98496*, 98499*, 98502*, 98503*, 99257*, 131166H*, 133979*, 133981*, 133990*, 133991*, 133993*, 134000*, 134030*, 147504*, 147505*, 176366*, 181487*, 181490*, 181491**, 181492*, 182958*, 209129*, 209130*, 214713*, 214714*, 214717*, 214719*, 214724*, 215130*, 246973*, 247709*, 255871*, 260323*, 261315*, 261316*, 261317*, 261321*, ANSP 2540*, 2541*, 2542*, 4678*, 4679*, 4680*, 4681*, 4682*, 4683*, 4684*, 4685*, 4686*, 4687*, 4688*, 4689*, 4690*, 4691*, 4692*, 4693*, 4694*, 4695*, 4696*, 4697*, 4698*, 4699*, 4700*, 4701*, 4702*, 4703*, 4704*, 4705*, 4706*, 4707*, 4708*, 4709*, 4710*, 4711*, 4712*, 13961*, 14266*, 14302*, 17125*, 17126*, 19147*, 19410*, 19411*; BMNH 77435*, 271169*, 734235*, 805678*, 4411813*; FMNH 18911*, 20199**, 20846*, 20847*, 21399*, 21400*, 21401*, 21402*, 21592*, 21676*, 28318*, 28319*, 28320*, 28321*, 28322, 28323*, 28324*, 28325*, 28326*, 34330*, 34681*, 34682*, 34683*, 34684*, 34685*, 34686*, 34687*, 34688*, 41194*, 41195*, 41196*, 41197*, 41198*, 41199*, 41200*, 41201**, 41202**, 41203*, 41225*, 41238*, 50887*, 50888*, 52335*, 54328*, 58757*, 64291*, 69602**, 69603*, 69604*, 69605**, 70728**, 70729**, 70730*, 70731**, 70732**, 70733**, 70734*, 70735**, 70736*, 70737*, 70738*, 70739*, 70740*, 78403*, 79869*, 79870*, 79871*, 79872*, 79873*, 79874*, 84210**, 84241*, 86764**, 86747**, 86749**, 86750**, 86849**, 86910*, 86911*, 86912*, 86913*, 87853*, 87854*, 87855**, 88875*, 88876*, 88877*, 88878*, 88879*, 88880*, 88881*, 89232*, 89233**, 89234*, 89235**, 92206*, 92207*, 92208*, 92209*, 92210*, 92211*, 92212*, 93170*, 93171*, 93172**, 93663*, 93664*, 94221*, 94322*, 94323*, 94325*, 94326*, 94327*, 94328*, 96002*, 98082*, 119373*, 119374*, 119375*, 119376*, 119377*; FSM 20658*; LACM 27367*, 27368*, 27370*, 54507*, 56765*, 56766*; MCZ 999*, 1000*, 1001*, 8017*, 28094*, 29615*, 30975*, 30976*, 30978*, 30979*, 30981*, 30982*, 32046*, 32047*, 32048*, 52579*, 52580*, 52581*, 52586*, 52604*, 52606*; MSUM 8575**, 8576**, 8577**, 9346**, 9347**, 9348**, 9349**, 9350**, 10692**, 11920**, 11921**, 11937**, 14369**, 14370**, 14371**, 14372**; MVZ 62688*, 121211*, 135822*, 153639*, 153640*, 153641*, 153642*, 155209*, 155210*, 155211*; USNM 526*, 4657*, 149000*, 172992**, 172991**, 172993*, 238671*, 241335**, 241336*, 241337*, 241338*, 255127*, 255128*, 255129*, 255130**, 255131*, 259480*, 270365*, 270366**, 281513*, 283471**, 309084*, 362119**, 374835*, 374836**, 374837*, 374838*, 388316*, 388236**, 406823*, 406824*, 406825**, 460075*, 544416*, 544417*, 544418**, 544419*, 546101**, 546102*, 546103*.

N. narica.—AMNH 1424*, 6676*, 7124*, 7125*, 12037**, 14330*, 14332*, 17256*, 18901**, 19210**, 23278, 24001*, 24639*, 24644*, 25191*, 25199*, 25201*, 25202*, 25207*, 25255*, 25841*, 25842*, 25843*, 26182*, 27251*, 28433*, 28434*, 28489*, 29438*, 29439*, 29599*, 29600*, 29830*, 30880*, 37626*, 38097*, 38100*, 38187*, 68525**, 70110*, 72195*, 123276**, 123277**, 123278**, 126182**, 126183**, 135970**, 139317*, 141854**, 141855**, 141977**, 143968**, 145151**, 145152**, 145153**, 145157**, 145200**, 145650**, 145651**, 145652**, 145653*, 145932**, 145933**, 145935*, 145936**, 145940**, 145942**, 145943**, 145944*, 145946**, 145947**, 145960**, 149144**, 165973**, 171905*, 172191**, 172192**, 172194**, 173530**, 176653*, 176657*, 206832*; ANSP 13631**, 17902*, 17903**, 18856*, 18857*, 18916*, 18917*, 18918*, 18919*, 19791*, 19792*, 20009*; BMNH 2702*; CAS 6429*, 7233**, 14824**, 15087*, 15088*; FMNH 253*, 11700*, 13252*, 13253*, 13254*, 13255*, 13256*, 13257*, 13258*, 13260*, 13261*, 14011*, 14012*, 14013*, 14014*, 14471*, 15543*, 30736*, 51101*, 58561*, 63904**, 63905*, 64445*, 66963*, 66964*, 66965*, 66966*, 66967*, 69599**, 69600**, 69610**, 106849*, 14178*, 14404*, 14826*, 15985*, 30737*, 35169**; FSM 6792*, 6858*, 12303*; KU 876*, 11989**, 11990**, 19256*, 24873*, 26954**, 29985**, 29986**, 33421*, 39187*, 63118**, 65928**, 65932*, 68056*, 68614*, 68616*, 71925*, 81537*, 83381*, 89904*, 92566*, 92676*, 104496*, 115604*; LACM 8823*, 9112*, 14350*, 24826*, 24835*, 29312*, 30099*, 30340*, 33251*, 33252*, 36056*, 56410*, 59442*, 59443*, 59444*, 59445*, 59446*, 59447*, 59448*; LSUMZ 2757**, 2758*, 2760**, 7286**,

Appendix 2.—Continued.

13381*; MCZ 5723**, 6418**, 7020**, 9090**, 10123**, 10124**, 10125**, 12456**, 29042**, 34338**, 41313**, 42788*; MSUM 3564*, 5679*, 9203**, 16374*, 16536**, 20618*, 23043*, 23044*; MVZ 23840*, 95049*, 98257*, 98258*, 98259**, 98260**, 98261*, 98262*, 98263*, 98264*, 98265*, 106048*, 106049*, 106050*, 109604*, 116822*, 118877*, 132107*, 132108*, 132109**, 132110**, 132111**, 132112**, 132113*, 132114**, 132115*, 132116*; TTU 13505*, 17488*; UANL 3721; USNM 983*, 6213*, 6214*, 6215*, 6821**, 7228*, 7230*, 8976**, 9069*, 9375*, 11405*, 12193*, 12194*, 12195*, 12757*, 12878*, 14194**, 15942*, 15970**, 16088*, 19506*, 20918*, 20919*, 32628*, 32629*, 32630*, 32631*, 32632*, 32651*, 32652*, 32653*, 33032*, 33270*, 33271*, 33272*, 33273*, 33274*, 33275*, 33276*, 33277*, 33278*, 33520*, 33521*, 33522*, 33523*, 33524*, 33525*, 33797*, 33798*, 34337*, 34408*, 34409*, 34923*, 37282**, 37284**, 37287**, 38137**, 44553**, 45276*, 45277**, 45278**, 45279**, 45280**, 45281**, 45283**, 45567**, 45568**, 45570**, 46428**, 51331**, 54983**, 60366**, 61204*, 61259**, 61260**, 61261*, 61262*, 61263*, 61264*, 68168*, 68194*, 73324*, 73325*, 74680**, 74681**, 88144**, 88145*, 88146*, 96214**, 96828*, 96829**, 96830*, 96831*, 96832*, 96833**, 98075**, 100412**, 100413**, 100414**, 100415*, 100528**, 108308*, 108309**, 108310**, 108311*, 108312**, 108313**, 108315**, 108519**, 108525**, 108537**, 116753**, 116754**, 126146*, 126147**, 126148**, 126149**, 126151**, 126152*, 126153*, 126154*, 126155*, 126705**, 127531**, 127532**, 127533**, 170894*, 171671**, 173071**, 179975**, 239116**, 239348**, 239349**, 239350**, 244896**, 244897**, 244898*, 244899*, 244900*, 245424**, 257314**, 257353*, 261435*, 261661**, 265662*, 265936*, 265937*, 268902*, 271095**, 271136**, 275666**, 284936*, 287488*, 287489*, 287490*, 290671**, 290672**, 296339**, 296340**, 304659**, 304660*, 307015*, 307016**, 307017**, 307018**, 307019**, 307020**, 307021**, 307022*, 309224**, 309225**, 310658**, 310659**, 310660*, 310661**, 314547**, 316212*, 316213**, 318178*, 324284**, 324285**, 324286**, 324287**, 324288**, 324289**, 334544*, 334545**, 334546*, 334547*, 334548*, 334549*, 334550*, 334666*, 336217**, 336218**, 337817*, 337818*, 337819**, 338347*, 340742*, 340743**, 340744**, 360453**, 503822*, 511711*, 520614**, 520615*, 541322*, 541394*.

N. nelsoni.—KU 876**, 92570**; MCZ 55722**; USNM 14808*, 14809*, 108520**, 108521*, 108522**, 108523**, 108524*, 108615*.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 387–398

A NEW SPECIES OF *CHROTOMYS* (RODENTIA: MURIDAE) FROM LUZON ISLAND, PHILIPPINES

Eric A. Rickart and Lawrence R. Heaney

Abstract.—A new species of *Chrotomys* (*C. gonzalesi*) is described from Mount Isarog on the Camarines Peninsula of southeastern Luzon Island, Philippines. It is one of four species of murid rodents confined to high elevation forest on this mountain. The new species is distinguishable from congeners by its relatively lower braincase, broader mastoid region, broader palate, and darker pelage. Data suggest that the new species is semifossorial, active both day and night, and feeds on annelid worms and soft-bodied arthropods. This discovery supports a general pattern of vicariant speciation between the highlands of northern and southern Luzon.

The murid rodent fauna of northern Luzon Island in the Philippines is a spectacular example of ecological and morphological radiation in isolation. Oldfield Thomas (1895, 1898) first described this remarkable fauna, which includes such diverse species as: *Phloeomys pallidus,* the arboreal giant cloud rat; *Rhynchomys soricoides,* the long-snouted shrew-rat; and *Chrotomys whiteheadi,* a species noteworthy for its pelage marked by a unique pattern of prominent dorsal stripes. Additional information on *Chrotomys* did not appear until a half-century later, when Kellogg (1945) named the subspecies *C. whiteheadi mindorensis* based on one specimen from southwestern Mindoro Island. Subsequently, Musser et al. (1982) examined additional specimens from Luzon and Mindoro and recognized two species, *Chrotomys whiteheadi* from the highlands of northern Luzon and *C. mindorensis* from lowland regions in southern Mindoro and central Luzon.

The diverse Philippine fauna, with its attendant potential for furthering our understanding of evolutionary dynamics of archipelagic communities, is severely threatened by habitat destruction. In the Philippines as a whole, primary forest cover has been reduced from more than 80% of total area at the turn of the century to about 8% currently (Myers 1988). Our current studies address evolutionary biogeography, patterns of diversity, and conservation biology of Philippine mammals (e.g., Heaney 1986, Heaney & Heideman 1987, Heaney & Rickart 1990).

To these ends, between March and May 1988, we surveyed mammals in Mount Isarog National Park on the Camarines Peninsula of southeastern Luzon Island (Rickart et al. 1991). Rising to 1966 m and surrounded by lowland plains, Mount Isarog is an extinct volcano that is the highest and most isolated forested peak in southern Luzon (Goodman & Gonzales 1990). This isolation evidently has led to the development of a distinctive mammal fauna. In 1961, an expedition to the mountain, led by D. S. Rabor of Silliman University, obtained a small collection of murid rodents that included the new genus and species *Archboldomys luzonensis* (Musser 1982) and the new species *Rhynchomys isarogensis* (Musser & Freeman 1981). During our 1988 survey, we obtained eight examples of a third species of *Chrotomys* that we name and describe in this report. The diagnosis of the

Mount Isarog *Chrotomys* is placed in the context of comparisons to *C. mindorensis* and *C. whiteheadi,* and to *Celaenomys silaceus,* the presumed sister-group of the genus *Chrotomys* (Heaney & Rickart 1990).

Specimens Examined and Methods

Specimens examined in this study are deposited at the American Museum of Natural History, New York (AMNH), Field Museum of Natural History, Chicago (FMNH), Bell Museum of Natural History, University of Minnesota, Minneapolis (MMNH), and United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The following comparative samples were used: *Chrotomys whiteheadi* (6).—LUZON: Mountain Province, Mount Data region (AMNH 18513; FMNH 62281, 62282; USNM 102547, 102548, 102552); *Chrotomys mindorensis* (10).—LUZON: Laguna Province, Los Baños, International Rice Research Institute (USNM 536800–536802); Nueva Ecija Province, San Jose, south of Manikla (USNM 399581); Pampanga Province, Clark Air Base (USNM 356390); Tarlac Province, San Miguel, Concepcion (USNM 349048–349050); MINDORO: Mindoro Occidental Province, 3 mi, SSE San Jose, Central (USNM 277639, holotype); Mount Iglit Station (MMNH 12972); *Celaenomys silaceus* (2).—LUZON: Mountain Province, Mount Data region (FMNH 62286, 62287).

External measurements were recorded from specimen labels or from field notes of collectors. If external measurements were missing, length of hind foot (including claws) was measured from fluid-preserved specimens or study skins. Thirty-nine cranial, mandibular, and tooth dimensions, recorded to the nearest 0.1 mm using dial calipers, were measured on adult specimens, and tooth measurements were taken on young specimens with fully erupted permanent dentition. Limits of measurements follow the protocol of Musser (1979), with the following exceptions: condylobasal length—anterior edge of premaxilla to posterior margin of occipital condyle; palatal length—anterior edge of premaxilla to posterior margin of bony palate; mastoid breadth—greatest width across mastoid processes; condylar breadth—greatest width across occipital condyles; breadth of braincase—least width immediately behind zygomatic arches; orbital length—most anterior point in orbit to most posterior point on inner margin of zygomatic arch in temporal fossa; breadth of nasals—greatest width across nasals; length of rostrum—anterior edge of premaxilla to most anterior point in orbit; depth of rostrum—anterior edge of incisive foramina to nearest point on dorsal surface of nasals; palatal breadth—greatest width across crowns of maxillary toothrows; length of mandibular toothrow—alveolar length from anterior margin of m1 to posterior margin of m3; length of lower incisor—anterior margin of incisor alveolus to incisor tip (not along curve); length of mandible—greatest length from anterior margin of incisor alveolus to posterior edge of condyle; height of mandible—greatest height from coronoid process to angular process; depth of mandibular ramus—alveolus at middle of m1 to nearest point on ventral edge of mandible; size of molars—greatest length and width of crowns of each upper and lower molar.

Student's *t*-test was used to assess differences between group means for cranial and external measurements. To provide a general quantitative description of cranial and mandibular variation among specimens, principal components analysis was performed on log-transformed measurements using the correlation matrix. Data were analyzed by Statistical Analysis System programs (SAS Institute, Inc. 1985) on a desktop microcomputer.

Results

Chrotomys gonzalesi, new species
Figs. 1–2

Holotype.—USNM 458952, adult male collected on 28 April 1988 (original number 4176 of L. R. Heaney); skull with carcass preserved in fluid. The right occipital region of the skull is slightly damaged, otherwise the specimen is in excellent condition. The holotype is currently deposited in the USNM but will be transferred to the Philippine National Museum, Manila.

Type locality.—Western slope of Mount Isarog, 4 km N, 21 km E Naga, Camarines Sur Province, Luzon Island, Philippines, 1350 m elevation, 13°40′N, 123°22′E.

Distribution.—Known only from primary forest on the western slope of Mount Isarog, between 1350 and 1750 m elevation.

Referred specimens.—In addition to the holotype, there are seven other specimens (USNM 458951, 458953–458958) collected during March and April 1988, on the western slope of Mount Isarog between 1350 and 1750 m elevation. Five of these consist of skulls with carcasses in fluid, and two are whole carcasses in fluid.

Etymology.—Named in honor of Pedro C. Gonzales of the Philippine National Museum, in recognition of his devotion to the study and conservation of Philippine birds and mammals.

Diagnosis.—A medium-sized rat (mean weight of adults 136 g) similar to other *Chrotomys* in size and general body proportions (Table 1). Distinguishable from *C. mindorensis* by its generally darker dorsal coloration, less prominent medial stripe, proportionately shorter tail, proportionately smaller plantar pads, lower braincase, broader mastoid region, broader palate, shorter and thinner mandible, and longer lower incisors. Distinguishable from *C. whiteheadi* by its darker dorsal coloration, broader and deeper rostrum, lower braincase, broader mastoid and interorbital regions, broader palate, larger auditory bulla, and larger molariform teeth.

Description.—*Chrotomys gonzalesi* (Fig. 1) has the general morphology of a semifossorial rodent. The body is stout and cylindrical, with short, strong limbs and large forefeet armed with strong claws. Pelage is soft, dense, and fluffy; hairs average 15 mm long mid-dorsally. Predominant dorsal color from snout to tail is shiny black, with faint brown highlights. Individual hairs are bicolored, with basal one-third dark gray and the remainder black. In most specimens a pale yellowish buff medial stripe extends from the forehead to the base of the tail. In others the stripe is faint, discontinuous, and confined to the head and upper back. Hairs comprising the medial stripe are similar to those of adjoining black areas, but have pale tips 2–3 mm long. Mid-lateral pelage also is yellowish buff, darker over the shoulders and flanks. Transition between lateral and dorsal color is gradual, and there is no sharp transition between the color of the sides and underparts. Underparts are dark gray, faintly washed with grayish buff, particularly at the sides. Three specimens have a white blaze along the midline on the chest or upper abdomen. Aside from the region of the medial stripe, the top of the head is blackish to the snout. Lips are silvery gray blending to yellowish buff on the cheeks and side of head. Mystacial vibrissae are blackish gray. There is no eye ring. Pinnae are pale gray, nearly naked on the anterior surface but with a sparse covering of short gray hairs on the posterior surface. Dorsally, the metapodials are dark gray, covered with short dark hairs. Digits are pale and naked. The fore feet are relatively large, and are modified for digging. With the exception of the pollex, the digits are long and strong, the longest being the third. The pollex has a short, thick nail, whereas the other digits bear long, thick, nearly straight claws. The palmar surface is naked and unpigmented, with three small interdigital and two large metacarpal pads.

Table 1.—Cranial, dental, and external measurements of *Chrotomys gonzalesi, C. whiteheadi, C. mindorensis,* and *Celaenomys silaceus.* Probability statements are for equality of means for *C. gonzalesi* as opposed to *C. whiteheadi* (P1), *C. mindorensis* (P2), and *Celaenomys* (P3), respectively.

	Chrotomys gonzalesi				*Chrotomys whiteheadi*		
		Total sample					
Measurement	Holotype	Mean ± *SD*	Range	*n*	Mean ± *SD*	Range	*n*
Condylobasal length	41.9	39.8 ± 1.9	38.7–41.9	3	40.4 ± 1.1	39.3–42.0	4
Diastema length	15.8	14.8 ± 0.9	14.0–15.8	4	14.9 ± 0.5	14.3–15.5	5
Incisive foramina length	4.0	4.1 ± 0.3	3.9–4.5	4	4.7 ± 0.2	4.5–5.0	5
Incisive foramina breadth	2.3	2.1 ± 0.1	2.0–2.3	4	2.2 ± 0.1	2.1–2.3	5
Palatal length	23.1	22.1 ± 1.1	21.0–23.1	4	22.2 ± 0.6	21.4–23.2	5
Post-palatal length	15.9	15.2 ± 0.5	14.8–15.9	4	15.5 ± 0.5	14.8–15.8	4
Length of bulla	5.8	5.8 ± 0.1	5.7–5.9	5	5.4 ± 0.2	5.2–5.7	5
Mastoid breadth		13.2 ± 0.2	13.0–13.4	3	12.2 ± 0.3	11.9–12.6	5
Condylar breadth		10.1 ± 0.4	9.8–10.5	3	9.7 ± 0.3	9.6–10.0	5
Height of braincase	11.5	11.5 ± 0.1	11.3–11.6	5	11.8 ± 0.2	11.6–12.1	3
Breadth of braincase	15.7	15.9 ± 0.1	15.7–16.0	4	15.7 ± 0.2	15.5–15.8	3
Zygomatic breadth	22.4	21.4 ± 0.8	20.4–22.4	4	21.7 ± 0.3	21.5–22.0	3
Interorbital breadth	7.7	7.8 ± 0.1	7.7–7.9	5	7.3 ± 0.2	7.1–7.5	4
Orbital length	14.6	13.7 ± 0.7	12.8–14.6	5	13.4 ± 0.7	12.7–14.1	4
Length of nasals	13.6	13.0 ± 0.6	12.2–13.6	4	12.7 ± 0.4	12.3–13.2	5
Breadth of nasals	3.8	3.7 ± 0.2	3.4–3.9	4	3.6 ± 0.3	3.2–3.9	5
Length of rostrum	18.1	17.4 ± 0.7	16.8–18.1	4	17.6 ± 0.4	17.1–18.1	5
Breadth of rostrum	8.8	8.4 ± 0.3	8.1–8.8	4	7.9 ± 0.2	7.6–8.2	5
Depth of rostrum	8.0	7.6 ± 0.3	7.4–8.0	4	7.2 ± 0.2	7.0–7.4	5
Zygomatic plate breadth	3.3	3.1 ± 0.2	2.9–3.3	5	3.1 ± 0.2	3.0–3.3	5
Maxillary toothrow length	6.0	6.2 ± 0.2	6.0–6.4	6	5.6 ± 0.2	5.3–5.7	4
Palatal breadth	8.1	8.1 ± 0.1	8.0–8.3	5	7.2 ± 0.3	7.0–7.7	5
Mandibular toothrow length	6.5	6.5 ± 0.1	6.4–6.6	6	5.6 ± 0.3	5.5–6.0	5
Lower incisor length	9.6	9.6 ± 0.4	9.1–10.1	5	9.5 ± 0.7	8.5–10.2	5
Length of mandible	26.1	25.2 ± 0.9	24.1–26.1	5	25.0 ± 0.7	24.3–26.0	5
Height of mandible	11.4	10.9 ± 0.5	10.4–11.4	5	11.6 ± 0.3	11.1–11.8	5
Depth of mandibular ramus	5.3	5.1 ± 0.2	4.8–5.4	5	5.3 ± 0.4	4.8–5.8	5
M1 length	3.5	3.6 ± 0.1	3.4–3.7	6	3.0 ± 0.1	2.9–3.3	6
M1 width	1.9	1.8 ± 0.1	1.7–1.9	6	1.6 ± 0.1	1.5–1.6	6
M2 length	2.0	2.2 ± 0.1	2.0–2.3	6	2.0 ± 0.1	1.9–2.2	6
M2 width	1.7	1.8 ± 0.1	1.7–1.8	6	1.5 ± 0.1	1.4–1.6	6
M3 length	0.7	0.8 ± 0.1	0.7–1.0	6	0.70		2
M3 width	1.0	1.0 ± 0.1	1.0–1.1	6	0.8 ± 0.1	0.7–0.9	2
m1 length	3.3	3.3 ± 0.1	3.2–3.4	6	2.9 ± 0.1	2.8–3.0	5
m1 width	1.8	1.8 ± 0.1	1.7–1.8	6	1.5 ± 0.1	1.4–1.6	5
m2 length	2.1	2.1 ± 0.1	2.1–2.2	6	1.7 ± 0.1	1.6–1.8	5
m2 width	1.7	1.7 ± 0.1	1.7–1.8	6	1.5 ± 0.1	1.4–1.5	5
m3 length	1.0	1.0 ± 0.1	0.9–1.1	6	0.9 ± 0.1	0.8–0.9	5
m3 width	1.1	1.1 ± 0.1	1.0–1.2	6	0.9 ± 0.1	0.7–1.0	5
Head-body length	189	173 ± 11	160–190	7			
Tail length	104	98 ± 7	89–105	7			
Hind foot length	37	37 ± 1	35–39	7	36 ± 1	35–38	5
Ear length	23	22 ± 1	20–23	7			
Weight (g)	190	136 ± 35	100–190	7			

Table 1.—Extended.

Chromtomys mindorensis			*Celaenomys silaceus*					
Mean ± *SD*	Range	*n*	Mean ± *SD*	Range	*n*	*P*1	*P*2	*P*3
40.9 ± 1.0	40.1–42.8	7	37.8 ± 1.2	37.0–38.7	2	>0.50	>0.20	>0.20
14.8 ± 0.4	14.3–15.3	7	13.9 ± 0.1	13.8–14.0	2	>0.50	>0.90	>0.10
4.0 ± 0.3	3.5–4.4	7	4.2 ± 0.1	4.1–4.2	2	<0.01	>0.40	>0.50
2.2 ± 0.1	2.1–2.4	7	1.8 ± 0.2	1.7–2.0	2	>0.20	>0.10	>0.10
22.5 ± 0.6	21.9–23.5	7	20.3 ± 0.6	19.9–20.7	2	>0.50	>0.20	>0.05
15.6 ± 0.5	15.1–16.6	7	14.6 ± 0.7	14.1–15.1	2	>0.20	>0.20	>0.20
5.9 ± 0.1	5.7–6.1	7	5.0 ± 0.1	4.9–5.0	2	<0.02	>0.20	<0.001
12.5 ± 0.2	12.1–12.8	7	11.2 ± 0.4	10.9–11.4	2	<0.01	<0.01	<0.01
9.9 ± 0.3	9.5–10.4	7	9.3 ± 0.3	9.1–9.5	2	>0.10	>0.40	>0.05
12.2 ± 0.3	11.7–12.6	7	11.6 ± 0.2	11.5–11.8	2	<0.05	<0.001	>0.10
16.0 ± 0.2	15.8–16.2	7	14.8 ± 0.1	14.8–14.9	2	>0.20	>0.10	<0.001
21.6 ± 0.6	20.9–22.5	7	18.7 ± 0.4	18.4–19.0	2	>0.50	>0.50	<0.02
7.4 ± 0.3	6.9–7.7	7	6.8 ± 0.1	6.7–6.8	2	<0.001	>0.05	<0.001
13.5 ± 0.4	13.0–14.1	7	12.4 ± 0.2	12.3–12.6	2	>0.90	>0.50	>0.05
13.2 ± 0.5	12.3–14.1	7	12.2 ± 0.4	12.0–12.5	2	>0.20	>0.40	>0.10
3.9 ± 0.2	3.7–4.2	7	3.1 ± 0.1	3.0–3.2	2	>0.50	>0.10	<0.05
17.7 ± 0.5	17.3–18.7	7	16.0 ± 0.6	15.6–16.4	2	>0.50	>0.90	>0.05
8.5 ± 0.3	8.1–8.8	7	6.6 ± 0.4	6.3–6.8	2	<0.05	>0.40	<0.01
7.7 ± 0.3	7.4–8.1	7	6.3 ± 0.4	6.0–6.6	2	<0.05	>0.40	<0.02
3.0 ± 0.2	2.6–3.2	7	3.0		2	>0.90	>0.50	>0.50
6.2 ± 0.4	5.8–6.6	7	4.3 ± 0.3	4.1–4.5	2	<0.01	>0.50	<0.001
7.8 ± 0.2	7.5–8.2	7	6.2 ± 0.1	6.2–6.3	2	<0.001	<0.02	<0.001
6.5 ± 0.4	5.9–7.2	7	3.7 ± 0.4	3.4–4.0	2	<0.001	>0.50	<0.001
8.1 ± 1.3	6.6–9.6	7	9.1		1	>0.90	<0.05	>0.20
26.2 ± 0.6	25.2–26.7	7	22.1 ± 0.8	21.5–22.7	2	>0.50	<0.05	<0.01
11.9 ± 0.3	11.5–12.4	7	10.5 ± 0.3	10.3–10.7	2	<0.05	<0.01	>0.40
5.5 ± 0.2	5.1–5.7	7	4.4 ± 0.1	4.4–4.5	2	>0.50	<0.02	<0.02
3.7 ± 0.2	3.4–4.0	7	2.5		2	<0.001	>0.20	<0.001
1.9 ± 0.1	1.8–2.0	7	1.3		2	<0.001	>0.50	<0.001
2.3 ± 0.2	2.1–2.6	7	1.6 ± 0.1	1.5–1.7	2	<0.02	>0.20	<0.001
1.9 ± 0.1	1.7–2.0	7	1.2 ± 0.1	1.2–1.3	2	<0.001	<0.02	<0.001
0.8 ± 0.2	0.6–1.2	7	0.6 ± 0.1	0.5–0.6	2	>0.20	>0.90	<0.05
1.1 ± 0.1	1.0–1.3	7	0.6 ± 0.1	0.5–0.7	2	<0.01	>0.05	<0.001
3.2 ± 0.2	3.0–3.5	7	2.4 ± 0.1	2.3–2.4	2	<0.001	>0.40	<0.001
1.8 ± 0.1	1.7–2.0	7	1.2		2	<0.001	>0.20	<0.001
2.0 ± 0.1	1.9–2.2	7	1.6 ± 0.1	1.5–1.6	2	<0.001	>0.05	<0.001
1.8 ± 0.1	1.7–1.9	7	1.2 ± 0.1	1.1–1.2	2	<0.001	>0.20	<0.001
1.1 ± 0.1	1.0–1.2	7				<0.02	<0.02	
1.2 ± 0.1	1.1–1.3	7				<0.01	>0.10	
167 ± 13	155–186	5	173		1		>0.40	>0.90
112 ± 11	99–123	5	116.5		1		<0.05	<0.05
38 ± 2	36–40	6	36.7 ± 0.2	36.5–36.8	2	>0.20	>0.20	>0.50
21 ± 2	19–23	4					>0.50	
172 ± 24	152–199	3					>0.10	

Fig. 1. Adult male *Chrotomys gonzalesi* (USNM 458952, holotype).

The plantar surface is naked, with pale gray pigmentation to the base of the toes. Four interdigital pads and one medial metatarsal pad (thenar) are well developed. A tiny lateral metatarsal pad (hypothenar) is present on five of the eight specimens (in two specimens only on one foot). Skin of the tail is pale gray dorsally, nearly white below, with a sparse covering of short blackish hairs. In some specimens the tail has a short (<1 cm) nearly white tip. Mid-dorsal tail scales are small (16–18 rows/cm) and roughly square. Three stiff, dark gray hairs about 2 mm long are associated with each scale. Females have two inguinal pairs of mammae.

The skull (Fig. 2) is wedge-shaped and robust, with a long, tapered rostrum, an expanded interorbital region, and a narrow braincase. Supraorbital and temporal surfaces are smooth and lack ridges. Nasals are short, terminating posterior to the incisor alveoli. Premaxillaries project only slightly beyond the anterior incisor faces. The interpremaxillary foramen is greatly enlarged. Incisive foramina are short and narrow, and are intersected by the premaxillary-maxillary suture near their posterior margins. The bony palate ends medial to the anterior margin of M3. Posterior palatine foramina are positioned between M1 and M2. There is a lateral alisphenoid strut separating the accessory foramen ovale from the masticatory-buccinator foramen. The auditory bullae are small and tightly attached to the squamosal. The squamoso-mastoid foramen is small. The mandible is long and thin, with a flattened, pitted region on the lower edge immediately behind the symphysis. The root of the lower incisor extends posteriorly into the condyloid process. Upper incisors are strongly procumbent, rounded in front, and ungrooved. Incisor enamel is pale, creamy yellow, forming a thin layer confined to the anterior surface of the tooth. The first two upper molars have moderately high cusps connected to form transverse laminar ridges. M3 is reduced to a simple peg without cusp definition. Upper molars lack posterior cingula. Both m1 and m2 have small posterior cingula.

Comparisons.—Specimens of *Chrotomys gonzalesi* are much darker than any *C. mindorensis* or *C. whiteheadi* examined. The darkened areas that form two dorsal stripes on the other species are much wider, so that specimens of *C. gonzalesi* appear to be generally blackish above, as opposed to predominantly brown or tan with a pair of nar-

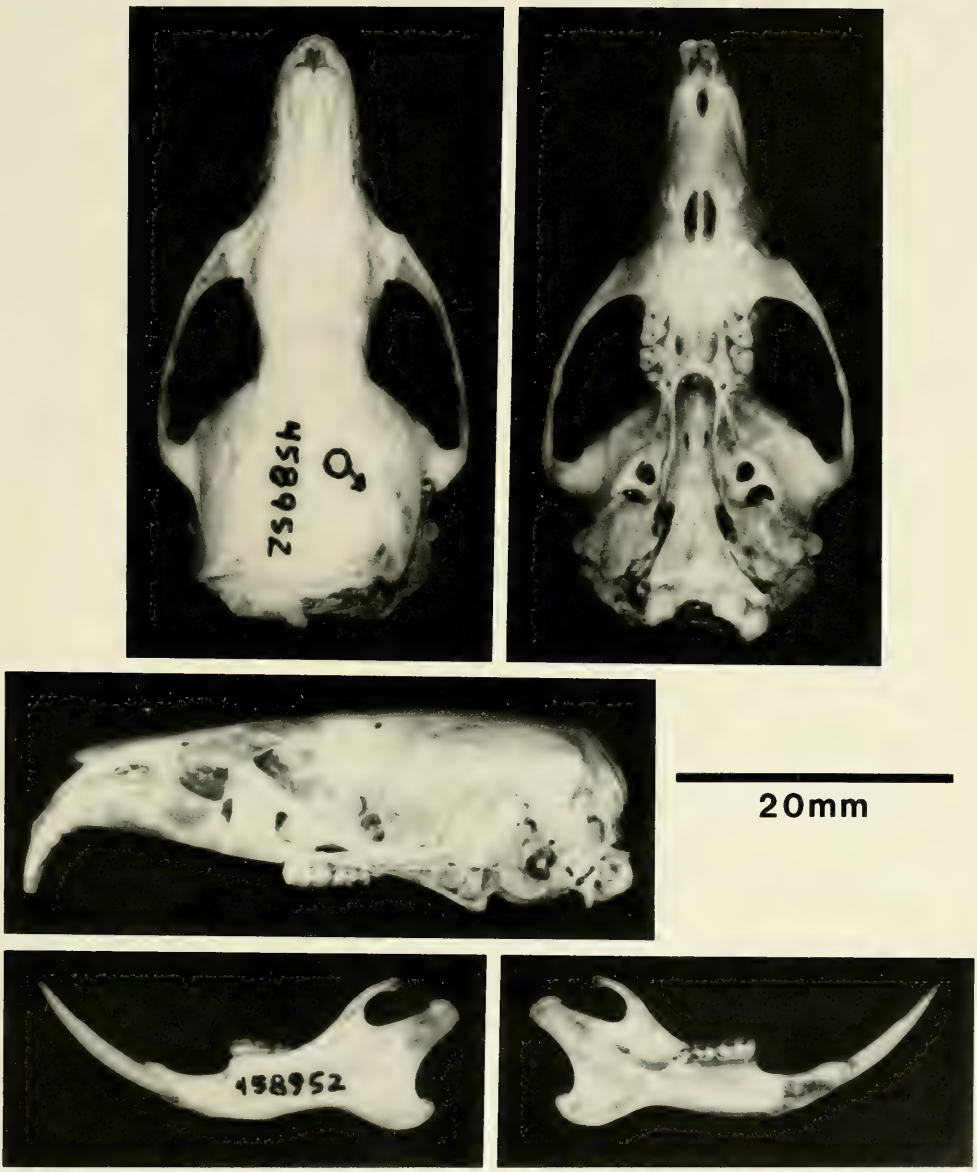


Fig. 2. Dorsal, ventral, and lateral views of cranium, and labial and lingual views of left mandible of *Chrotomys gonzalesi* (USNM 458952, holotype).

row black stripes (Musser et al. 1982). The blackish dorsal aspect of *Chrotomys gonzalesi* also differs from *Celaenomys,* which is dark gray with faint brown highlights, and is marked dorsally with a pale blaze on the forehead and (in some specimens) a faint line over shoulders. As in the other species of *Chrotomys, C. gonzalesi* has a pale mid-dorsal stripe. In some specimens, the narrow stripe extends from the forehead to the base of the tail, a configuration similar to that of *C. whiteheadi,* but different from the broader stripe of *C. mindorensis.* In other specimens the mid-dorsal stripe is faint and discontinuous. Lateral color is yellowish buff, similar to that of *C. mindorensis* but

different from the pale brown of *C. whiteheadi.* The pale lateral region is less extensive than in the other *Chrotomys* species. Underparts also are darker than in other species. Pelage of the new species is soft, dense, and long like that of *C. whiteheadi,* but different from the thinner and harsher pelage of *C. mindorensis* (Musser et al. 1982). The pelage of *Celaenomys* is softer, thicker, and shorter than that of *Chrotomys gonzalesi.* The tail of *C. gonzalesi* has pale gray scales with dark hairs as opposed to the brownish or brownish black scales with silvery hairs in the other species.

Body size is similar in all four species. The tail of *Chrotomys gonzalesi* is both proportionately and absolutely shorter than in either *Chrotomys mindorensis* or *Celaenomys silaceus* (Table 1). Tail length averages 56.5% (54.8–60.0%) of head-body length compared to 67.1% (56.9–76.4%) in *C. mindorensis* and 67.3% for one specimen of *Celaenomys.* Available specimens of *Chrotomys whiteheadi* lack external measurements; however, the skins appear to have relatively short tails. Measurements reported by Thomas (1895) for the holotype indicate a proportionate length of 56.6%, near the mean value for *C. gonzalesi* but below the range for *C. mindorensis.* Plantar pads of *Chrotomys gonzalesi* are substantially smaller than those on fluid-preserved specimens of *C. mindorensis.* The lateral metatarsal pad (hypothenar) is either rudimentary (five specimens) or absent (three specimens) in *C. gonzalesi,* whereas it is well developed in *C. mindorensis.* The plantar pads of both *Chrotomys whiteheadi* and *Celaenomys silaceus* have the same general arrangement, but their comparative size and the frequency of occurrence of the hypothenar cannot be determined from available material (no fluid-preserved specimens are known to us).

Cranial structure of *Chrotomys gonzalesi* is similar to that of the other members of the genus and to *Celaenomys.* However, there are significant differences between species for many measurements (Table 1). The skull of *Chrotomys gonzalesi* is larger than that of *Celaenomys,* with broader braincase, palate, mastoid region, interorbital region, and zygomatic arches, broader and deeper rostrum, and larger auditory bullae. In comparison to the other *Chrotomys* species, *C. gonzalesi* has a lower braincase, broader mastoid region, and wider bony palate. From *C. whiteheadi* it is further distinguished by its shorter incisive foramina, larger auditory bullae, broader interorbital region, and both broader and deeper rostrum (Table 1). The postglenoid vacuity between the auditory bulla and the squamosal bone is small in all three *Chrotomys* species, but is large in *Celaenomys.* Aside from this, no consistent differences among species in the size or positioning of cranial foramina were noted. The mandible of *Chrotomys gonzalesi* is similar to that of *C. whiteheadi,* but shorter and thinner than that of *C. mindorensis,* and longer and thicker than that of *Celaenomys.* Posterior height of the mandible is less than in the other species of *Chrotomys.* The exposed portion of the lower incisor is longer in *C. gonzalesi* and *C. whiteheadi* than in *C. mindorensis.* Although cheekteeth of all four species exhibit the same general cusp pattern, there are substantial differences in size. Molars of *C. gonzalesi* are nearly the same size as those of *C. mindorensis,* but are larger than those of both *C. whiteheadi* and *Celaenomys.*

A principal components analysis based on 14 cranial and mandibular measurements (Table 2) was conducted on a subset of 15 specimens on which all measurements could be taken. The first three components account for 85% of total variation. The first component, accounting for 58% of the variation, shows positive loadings of similar magnitude for most variables, indicating that it is primarily size that is represented. *Celaenomys* is distinguished from *Chrotomys* by low scores on this axis (Fig. 3), reflecting its smaller size.

Table 2.—Character loadings on first three components of principal components analysis using log-transformed cranial and mandibular measurements of 15 adult *Chrotomys* and *Celaenomys*.

Character	Component		
	1	2	3
Diastema length	0.249	0.364	0.282
Incisive foramina length	−0.042	0.283	0.552
Palatal length	0.308	0.254	0.013
Length of bulla	0.310	−0.188	−0.084
Height of braincase	0.148	0.182	−0.642
Interorbital breadth	0.245	−0.309	0.258
Length of rostrum	0.323	0.173	0.145
Depth of rostrum	0.333	−0.119	0.028
Zygomatic plate breadth	0.070	0.443	0.084
Maxillary toothrow	0.307	−0.272	−0.007
Palatal breadth	0.305	−0.250	0.157
Mandibular toothrow	0.314	−0.229	0.022
Mandible height	0.262	0.298	−0.238
Mandibular ramus	0.296	0.202	−0.135
Eigenvalue	8.131	2.248	1.565
Variance explained	58.1%	16.0%	11.2%

Component two (accounting for an additional 16% of total variation) contrasts individuals with long diastemas, incisive foramina, and bony palates, deep braincases and mandibles, narrow interorbital regions and bony palates, broad zygomatic plates, and short toothrows against individuals having the converse. Specimens of *Chrotomys whiteheadi* score high on this axis, those of *C. gonzalesi* and *C. mindorensis* score low, and those of *Celaenomys* are intermediate (Fig. 3). Component three (accounting for 11% of the variation) primarily contrasts individuals with long diastemas and incisive foramina, and shallow braincases against individuals with the converse. *Chrotomys gonzalesi* and *C. whiteheadi* have high scores, whereas *C. mindorensis* and *Celaenomys* have low scores on this axis (Fig. 3). All four taxa are fully separated from the others along at least one axis. There also is extensive overlap among *C. mindorensis* from Mindoro and Luzon, supporting the conclusion of Musser et al. (1982) that populations from the two islands are conspecific.

Ecology.—*Chrotomys gonzalesi* apparently is restricted to montane and "mossy" forest habitats (lower and upper montane rain forest habitats, sensu Whitmore 1984) above 1350 m elevation (Rickart et al. 1991). These habitats are characterized by a cool and wet climate year-round, steep slopes, and woody vegetation dominated by species in the families Fagaceae and Lauraceae (as opposed to the Dipterocarpaceae of lowland forests). The forest canopy varies from low (5 m) to moderate (20 m) and at higher elevations is broken by numerous treefalls. Vascular epiphytes and vines are abundant and the soil has a thick layer of humus. At 1750 m, thick layers of mosses and liverworts cover most subcanopy surfaces. Mosses are less common at 1350 m (Goodman & Gonzales 1990, Rickart et al. 1991).

Trapping data indicate that *C. gonzalesi* is uncommon where it occurs. In 4900 trap nights at sites at or above 1350 m, only eight specimens were obtained. In a comparable effort at lower elevations on Mount Isarog (4101 trap nights), no specimens were caught. Specimens were taken in Victor rat traps (seven animals) and a National live trap (one animal) set on the ground in areas

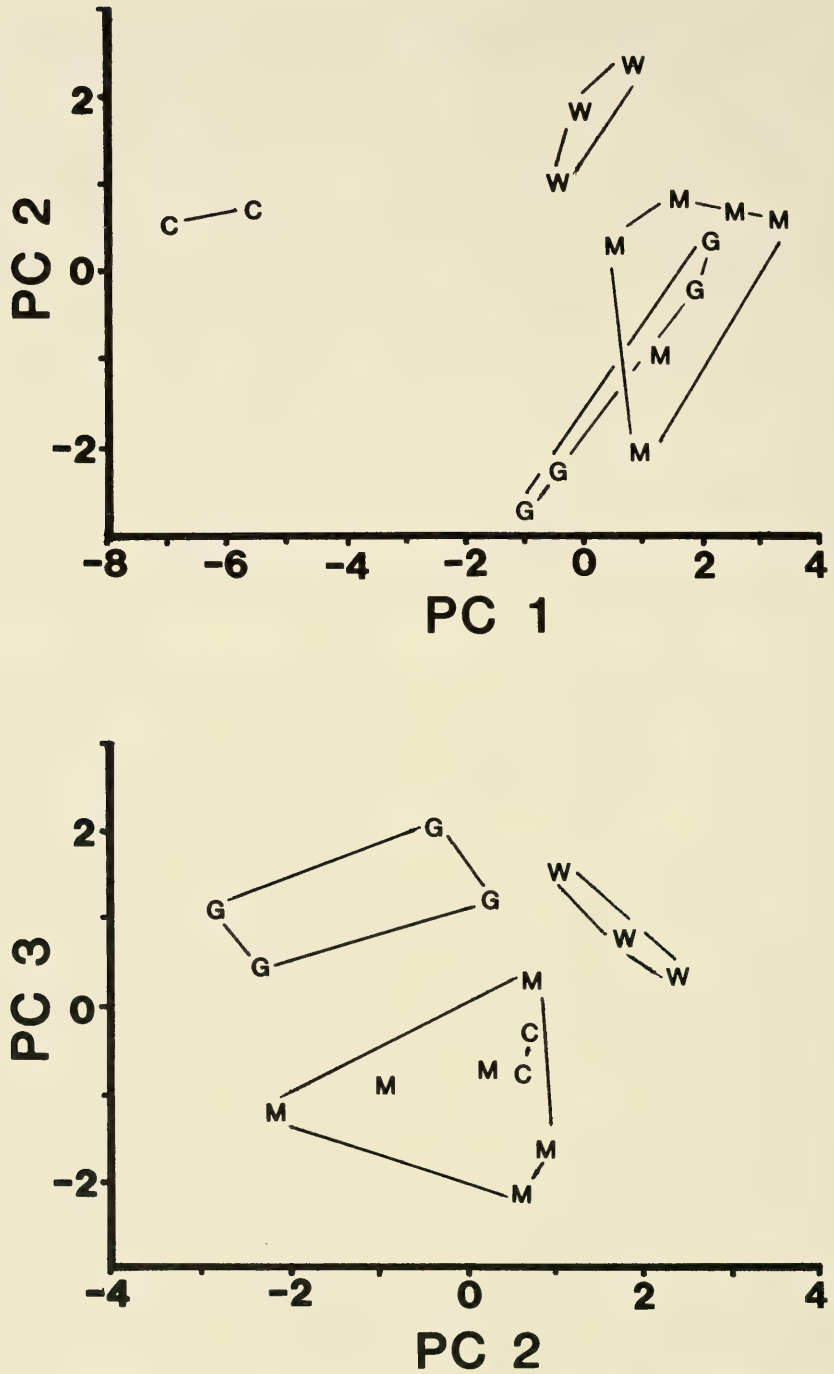


Fig. 3. Results of principal-component analysis of 14 cranial and mandibular measurements; scores for individual specimens are plotted on components 1 and 2 (top) and components 2 and 3 (bottom). C = *Celaenomys silaceus*, G = *Chrotomys gonzalesi*, M = *C. mindorensis*, and W = *C. whiteheadi*.

of heavy cover. Most individuals were caught along runways by fallen logs or in subsurface openings among exposed tree roots. Six animals were caught in traps baited with annelid worms, and two were taken in traps baited with fried coconut coated with peanut butter. Stomach contents of five snap-trapped specimens included (in order of decreasing frequency) remains of earthworms (Annelida: Megascolecidae), small terrestrial amphipods (Amphipoda), insect larvae (Coleoptera and Diptera), adult insects (Orthoptera and Diptera), and spiders (Araneida). None contained identifiable plant matter. Three individuals were trapped during daylight hours, one was caught at dusk, and four were trapped at night. Other small mammals trapped in close association with *Chrotomys gonzalesi* were *Crocidura grayi, Apomys musculus, Apomys* cf. *microdon, Archboldomys luzonensis,* an undetermined species of *Batomys, Rattus everetti,* and *Rhynchomys isarogensis* (Rickart et al. 1991).

Reproductive activity of *Chrotomys gonzalesi* was evident during the three months of field work. An adult female taken on 20 March had prominent teats and five placental scars (probably two sets). An adult female taken on 27 April contained two embryos in early development. Adult males trapped on 27 March and 28 April were in full breeding condition (scrotal testes, convoluted epididymides). Immature animals were caught in late March. A pregnant female and adult male were taken in the same trap on consecutive nights.

Discussion

Evidence from morphology, stomach contents, and trapping results indicates that *Chrotomys gonzalesi* is a semifossorial, primarily vermivorous species active day and night (Rickart et al. 1991). Presence of a pregnant female at the end of April and large immature animals in March suggests that the breeding season is relatively long. There is little information on ecology of the nearest relatives of *C. gonzalesi. Chrotomys whiteheadi* and *Celaenomys silaceus* occur in montane forest in the highlands of northern Luzon. The former includes earthworms in its diet and probably is ecologically similar to *C. gonzalesi* (Rabor 1955, Sanborn 1952). *Chrotomys mindorensis* occurs in a variety of lowland habitats in central Luzon and southwestern Mindoro (Barbehenn et al. 1973, Temme 1974); habitat differences suggest that it is ecologically distinct from the other species.

The discovery of *Chrotomys gonzalesi* supports the pattern of vicariant speciation between northern and southern Luzon that was postulated by Musser & Freeman (1981) on the basis of their description of *Rhynchomys isarogensis.* Both *Chrotomys gonzalesi* and *Rhynchomys isarogensis* apparently are restricted to high elevation forest on Mount Isarog, a habitat pattern shared with two other murid species endemic to the mountain (*Archboldomys luzonensis* and *Batomys* sp.). Extensive lowlands separate the highland forests of Mount Isarog from similar areas in northern Luzon that support *Chrotomys whiteheadi* and *Rhynchomys soricoides.* The mountain also is distant from the range of *Chrotomys mindorensis,* not known to occur south of Laguna Province (ca. 250 km WNW of Mount Isarog). During Pleistocene glacial periods when sea level was low and temperatures cooler (Heaney 1986, Heaney & Rickart 1990), montane forest probably extended further down into lowland regions allowing contact between populations now geographically and ecologically isolated (Musser & Freeman 1981). The rich endemic mammal fauna of Mount Isarog suggests that the Camarines Peninsula has experienced long periods of relative isolation from the main Luzon land mass. In this light, further studies of the murids of southern Luzon (including *Apomys, Batomys,* and *Phloeomys*) would be of interest, and a survey of other highland areas on the peninsula, particularly Mount

Bulusan (1559 m) at the southernmost tip of Luzon, would be informative.

Acknowledgments

We thank A. Batal, R. Buenviaje, D. Destajo, R. Fernandez, P. Gonzales, S. Goodman, F. Jumalon, M. Laranjo, M. Lepiten, J. Ramos, D. Samson, D. Schmidt, L. Tagat, and R. Utzurrum for assistance with field work; E. Birney, M. Carleton, and G. Musser for permission to examine specimens under their care; S. James for identification of earthworms; and L. Casjens, L. Gordon, B. Patterson, D. Schmidt, and G. Ungerman for technical assistance. W. Behle, M. Carleton, L. Hansen, G. Musser, and anonymous reviewers provided helpful comments on the manuscript. Field work was supported by National Science Foundation grant number BSR-8514223. A study visit by Rickart to Field Museum was supported by a grant from the Thomas J. Dee Fund.

Literature Cited

Barbehenn, K. R., J. P. Sumangil, & J. L. Libay. 1973. Rodents of the Philippine croplands.—Philippine Agriculturalist 56:217–242.

Goodman, S. M., & P. C. Gonzales. 1990. The birds of Mt. Isarog National Park, Camarines Sur, southern Luzon.—Fieldiana: Zoology, New Series 60:1–39.

Heaney, L. R. 1986. Biogeography of the mammals of Southeast Asia: estimates of colonization, extinction, and speciation.—Biological Journal of the Linnean Society 28:127–165.

———, & P. D. Heidman. 1987. Philippine fruit bats: endangered and extinct.—Bats 5:3–5.

———, & E. A. Rickart. 1990. Correlation of clades and clines: geographic, elevational, and phylogenetic distribution patterns among Philippine mammals. Pp. 321–332 *in* G. Peters & R. Hutterer, eds., Vertebrates in the tropics. Zoologisches Forschungsinstitut und Museum Alexander Koenig.

Kellogg, R. 1945. Two new Philippine rodents.—Proceedings of the Biological Society of Washington 58:121–124.

Musser, G. G. 1979. Results of the Archbold Expeditions. No. 102. The species of *Chiropodomys*, arboreal mice of Indochina and the Malay Archipelago.—Bulletin of the American Museum of Natural History 162:379–445.

———. 1982. Results of the Archbold Expeditions. No. 110. *Crunomys* and the small-bodied shrew rats native to the Philippine Islands and Sulawesi (Celebes).—Bulletin of the American Museum of Natural History 174:1–95.

———, & P. W. Freeman. 1981. A new species of *Rhynchomys* (Muridae) from the Philippines.—Journal of Mammalogy 62:154–159.

Musser, G. G., L. K. Gordon, & H. Sommer. 1982. Species-limits in the Philippine murid, *Chrotomys*.—Journal of Mammalogy 63:514–521.

Myers, N. 1988. Environmental degradation and some economic consequences in the Philippines.—Environmental Conservation 15:205–214.

Rabor, D. S. 1955. Notes on the mammals and birds of the central northern Luzon highlands, Philippines. Part I: notes on mammals.—Silliman Journal 2:193–218.

Rickart, E. A., L. R. Heaney, & R. C. B. Utzurrum. 1991. Distribution and ecology of small mammals along an elevational transect in southeastern Luzon, Philippines.—Journal of Mammalogy (in press).

Sanborn, C. C. 1952. Philippine Zoological Expedition 1946–1947. Mammals.—Fieldiana: Zoology 33:89–158.

SAS Institute, Inc. 1985. SAS user's guide: statistics. Version 5. SAS Institute, Inc., Cary, North Carolina, 956 pp.

Temme, M. 1974. Neue belege der Philippinischen streifenratte *Chrotomys whiteheadi* Thomas, 1895.—Zeitschrift für Säugetierkunde 39:342–345.

Thomas, O. 1895. Preliminary diagnoses of new mammals from northern Luzon, collected by Mr. John Whitehead.—Annals and Magazine of Natural History, Series 6, 16:160–164.

———. 1898. On the mammals obtained by Mr. John Whitehead during his recent expedition to the Philippines.—Transactions of the Zoological Society of London 14:377–412.

Whitmore, T. C. 1984. Tropical rain forests of the Far East. Second edition. Oxford University Press, Oxford, 352 pp.

(EAR) Utah Museum of Natural History, University of Utah, Salt Lake City, Utah 84112; (LRH) Division of Mammals, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605.

PROC. BIOL. SOC. WASH.
104(2), 1991, pp. 399–415

THE MAMMALS OF CATANDUANES ISLAND: IMPLICATIONS FOR THE BIOGEOGRAPHY OF SMALL LAND-BRIDGE ISLANDS IN THE PHILIPPINES

Lawrence R. Heaney, Pedro C. Gonzales, Ruth C. B. Utzurrum and Eric A. Rickart

Abstract.—Thirty-five species of mammals are known from Catanduanes Island, 28 of which are reported here for the first time; these include 1 insectivore, 24 bats, 1 primate, 5 rodents, 2 carnivores, and 2 ungulates. No endemic species are present, and all but one (the widespread *Saccolaimus saccolaimus*) are known from neighboring Luzon. All populations are morphologically similar to conspecifics on Luzon. Data are consistent with the prediction (based on depth of surrounding water) that Catanduanes should exhibit characteristics associated with being a small land-bridge island of the Luzon faunal region. The avifauna of Catanduanes shows similar biogeographic patterns.

Although the mammalian fauna of Luzon Island is considered to be one of the best-known in the Philippine Archipelago, none of the small islands offshore of Luzon had been comprehensively surveyed at the time of the last faunal review (Heaney 1986, Heaney et al. 1987). This is unfortunate, since knowledge of the faunas of small islands often provides the basis for inferences about the dynamics of evolution and extinction within island archipelagos (Case & Cody 1983, Heaney & Patterson 1986), and such studies within the Mindanao and Palawan regions of the Philippines have been productive (Heaney 1986, Heaney et al. 1989). Accordingly, the small islands surrounding Luzon (which has a rich fauna of endemic murid rodents and pteropodid bats) may be expected to be especially interesting for studies of evolutionary biogeography.

This paper reports the results of a survey of the mammals of Catanduanes Island, an island that lies adjacent to the southern peninsula of Luzon. Published records previously existed for only seven species of mammals (Heaney 1986). Because little has been published on the ecology of most species of small mammals in the Philippines, we include here data on reproduction and descriptions of habitats where the animals were taken. Geographic variation in most Philippines species is poorly documented, so we have provided external and cranial measurements wherever possible. We use these data to test several predictions of biogeographic patterns proposed earlier (Heaney 1986, Heaney et al. 1989).

Climate and Geology of Catanduanes

Catanduanes is an island of 1513 km^2 that lies 8 km east of the nearest portion of the southeastern peninsula of Luzon. Because the highest point is 764 m, the island is below the elevation required to support more than small and localized areas of montane or mossy vegetation (Heaney et al. 1989, Whitmore 1984). In about 1970, primary forest was estimated to cover about 25% of the island, with about half of the remaining area covered by secondary forest (observations by PCG). By 1988, the Philippine Bureau of Forest Development estimated that primary forest occupied about 5% of the island, with about 25% of the island covered by scattered patches of degraded primary and second-growth forest.

Catanduanes lies in one of the principal typhoon tracks in eastern Asia, and rainfall is thus both high and seasonal. Mean annual rainfall at Baras, Pandan, and Virac is 5481,

3149, and 2971 mm, respectively; there is no month of the year at any of these sites that receives less than 100 mm (Manalo 1956). Although our 1988 sampling period occurred during one of the drier times of the year, it rained nearly every day. For additional description of the island and a treatment of its avifauna, see Gonzales (1983) and Goodman & Gonzales (1989).

Catanduanes is a part of the Eastern Philippine Rim Structural Region, and lies just to the west of the northern portion of the Philippine Trench, where the Pacific Plate is actively subducted below the Philippines. Volcanic activity associated with this subduction has produced 1966 m (Mt. Isarog) and 2462 m (Mt. Mayon) basaltic/andesitic cones on southern Luzon, about 60 km to the west and southwest of Catanduanes. Although there are no volcanic products on Catanduanes, the island is subject to frequent earthquakes; we experienced one registered at 6.9 on the Richter scale during our 1988 season. Most of the island is composed of Cretaceous to Eocene shales and limestone that have been partially metamorphosed into schist and marble; some soft coal of the same age is present. The southern tip of the island is composed of Recent to Pleistocene corals, reef limestones, beach deposits, and marine sediments; these limestones contained the caves that we investigated. The present island mass was upraised during Pliocene to Recent times, in association with the tectonic activities that caused the development of the region's prominent volcanic cones (Hamilton 1979, Hashimoto 1981, Philippine Bureau of Mines 1963).

Current water depth separating Catanduanes from Luzon is about 50 m. It is therefore virtually certain that Catanduanes was a part of the island of Greater Luzon during the late Pleistocene (i.e., from about 25,000 to about 10,000 years ago), when sea level was about 120 m lower than at present (Heaney 1986).

Methods

Field studies were conducted during two periods. The first phase extended intermittently from May 1968 to June 1971; specimens were collected at four forest sites by PCG and a team from the Philippine National Museum in conjunction with studies of the avifauna of Catanduanes (Gonzales 1983). The second period of intensive mammal investigation extended from 12 to 28 February 1988; specimens were collected at two forest sites and two caves by a joint team from the United States National Museum of Natural History (USNM; Washington, D.C.), the Philippine National Museum (PNM; Manila), and Silliman University (SU; Dumaguete). Sampling during phase two followed methods used on Leyte, Negros and other islands in 1987 (Heaney et al. 1989) in order to facilitate comparisons.

During phase two, bats were caught in mist nets set on ridgetops, across trails and streams, at the edges of clearings adjacent to forest, and inside caves. Nets were tended continuously during the primary activity peak from early dusk (about 17:30) until about 21:00, and some were tended longer; nets were left open thereafter, and bats were removed at dawn. We also captured several *Miniopterus* spp. in Cave 1 in a butterfly net, and one *Hipposideros obscurus* from a hollow log in a fragment of a mist net. During the first phase, nets were examined in late afternoon and at dawn, and occasionally during the evening.

Non-volant small mammals were caught in traps; during the first phase all traps were Victor rat snap-traps (ca. 75%) and National live traps (ca. 25%). Phase two traps were baited late each afternoon with fresh fried coconut coated with peanut butter, and checked each morning soon after dawn; they were checked occasionally in the early afternoon and evening as well. Traps were placed 5 to 15 m apart; most (95%) were

placed on the ground, but ca. 5% were placed above ground on fallen trees, horizontal branches, large vines, etc. Trap lines were run for three to five days, usually four. Phase one traps were baited daily, and were handled in a fashion similar to that for phase two, but in a less standardized manner.

Temperatures during 1988 were recorded daily with minimum-maximum thermometers that were maintained in shaded spots about 1.5 m above the forest floor. Tree diameter at breast height (DBH) was estimated so as to exclude buttresses.

Voucher specimens were prepared in fluid, as skeletons, or as skins with partial skeletons, and have been deposited at the USNM and the PNM. In 1988, specimens were autopsied in the field for reproductive information. Size of embryos was measured as crown to rump length (CRL). Subadult animals are defined here as those that have not completed cranial growth, especially those having unfused basicranial sutures. Comments on distribution and use of scientific names are based on Heaney et al. (1987) unless stated otherwise. Records of specimens examined are summarized at the end of each account whenever this is not obvious within the account; such summaries include site number and number of specimens (in parentheses).

Comparison of fruit bat species richness and netting success from phase two sampling with data from other islands was standardized to exclude *Pteropus leucopterus* because we are often unable to sample the large flying foxes (*Acerodon* and *Pteropus*) that forage at the top of the forest canopy, and so have not included these species in other analyses (Heaney et al. 1989).

External measurements and weights reported here were taken by the authors in the field on fresh animals in 1988. All cranial measurements were taken by LRH with digital calipers graduated to 0.01 mm. Comparisons of cranial measurements are to published records of specimens also measured by LRH. Some comparisons were made with specimens in the University of Michigan, Museum of Zoology (UMMZ).

Study Sites

We surveyed mammals at six forest sites (four in 1969–1971 and two in 1988) and two caves sites (both in 1988); these are referred to in the species accounts by number. Additional minor sites are described in the species accounts.

Site 1 (2 days in May 1968).—Located in the municipality of Dugui-too, north of Virac at 300–400 m elevation in mixed primary forest, second growth, and recently logged areas.

Site 2 (2 days in June 1969).—Located in Barrio San Pedro, in Gigmoto Municipality, at 200–300 m in moderately to very steep terrain, in patchy primary forest, second growth with abundant *Musa* sp., and cultivated land along the Gigmoto River.

Site 3 (2 days in June 1969).—Located in Matamok Barrio in Caramoran Municipality, east of Caramoran at the top of a small promontory (ca. 200 m) in moderately steep terrain, in a mixture of low primary forest and second growth with patches of abaca (*Musa textilis*).

Site 4 (2 days in June 1971).—Located in Barrio Balinad in Viga Municipality, east of Viga in low rolling hills along the Balinad River (100–200 m) in patchy primary forest, second growth, and agricultural clearings.

Site 5 (8 days in 1988).—Located 8½ km W of Gigmoto at 250 m elevation (13°47′N, 124°19′E) in primary forest on a small plateau between two rivers. Ground slope was slight, rarely exceeding 20°. Temperatures ranged from nighttime lows of 20.5° to 23.5°C to daytime highs of 23.5° to 26.0°C, with daily temperature ranges of 1.5° to 4.5°C. The tallest trees (mostly dipterocarps, including *Shorea* sp.) in the sampling area were about 25 m and had large but-

tresses; the canopy was 15–20 m but was discontinuous because many of the trees with the largest diameters (DBH 1.0 to 1.3) were broken off at 20 to 25 m, giving the impression that the frequent typhoons often seriously damage the forest. Epiphytic vines, ferns, and orchids were common on upper branches of large trees; moss was present but rare. Scattered slender palms (*Livistona*) reached the canopy; we noted no fig (*Ficus*) trees. The broken canopy allowed much light to penetrate to the forest floor, and vegetation near the ground was heavy, with saplings, small ground palms, sapling *Livistona* palms, broad-leafed herbaceous plants, viny rattan, and many viny pandans (*Freycinetia* sp.) commonly represented, as well as a few scattered erect terrestrial pandans (*Pandanus* sp.) and wild bananas (*Musa* sp.). Fallen trees and portions of trees were common; leaf litter was light. A small clearing (ca. 1 ha) was located within our study site; no traps were set in the clearing, but 14 net-nights were from nets set at the edge.

Site 6 (7 days in 1988).—Located 8½ km W, 1 km N Gigmoto at 200 m elevation (13°48′N, 124°19′E) along the dirt road from Summit to Gigmoto that briefly parallels then crosses the Buadan River, within about 0.75 km of human habitation sites. The river was a clear, fast-moving stream, 5–10 m wide and up to 1 m deep in a rocky bed 10–20 m wide. The area was one of low hills, with banks along the river 20 to 40 m high and often steep (up to 60°, typically 45°). The forest was similar to that at Site 2, but logging and clearing for agriculture had left a mosaic of primary and secondary forest, second growth, and active fields. Tree height was similar, but the protected slopes along the river supported more unbroken large trees (up to 35 m), including figs (*Ficus*). Abaca (*Musa textilis*), wild banana (*Musa* sp.) and tree ferns (*Cyathea* sp.) were common in secondary forest and old fields. Traps and nets were set in all habitats.

Cave 1.—Luyan Cave, located 3 km E, ¾ km N of San Andres at an elevation of 80 m (13°36′N, 124°8′E), is along the main road from Virac to San Andres. The cave is in a region of rugged limestone ridges that occupies much of southern Catanduanes. Nearby vegetation was about half agricultural land and half heavily disturbed secondary forest, with forest predominating on the steep slopes near the cave. The entrance to the cave is a recreational area and a religious shrine, with concrete steps and flooring within the well-lit entrance area. The cave was about 300 m long, with entrances at both ends, and with a small side-passage; there was abundant evidence of flooding. The main passage was 8–10 (up to 15) m wide and usually 15 m high (up to 20 m). It was heavily disturbed by guano miners and bat hunters; the bats were skittish. The ceiling and walls were rather smooth, with some solution holes and stalactites.

Cave 2.—A small cave, located 4 km W of Virac in the barrio of Pajo at an elevation of 50 m (13°35′N, 124°11′E), is on a hillside adjacent to the Pajo River in a large limestone outcropping. Nearby vegetation was predominantly agricultural land (mostly rice fields), but heavily disturbed secondary forest occurred along the steep hillsides. The main entrance was small (2 m high × 1.5 m wide) and partly shrouded by bushes and bamboo. The cave was rather short (about 30 m long), with vertical height of 2–4 (rarely up to 5) m and width of 2–3 (rarely to 4) m. A second entrance lay at the opposite end of the cave; this entrance was small (0.5 × 0.5 m) and partly blocked by vegetation and rubble. Two side passages were present, one 5 m long and 4 m wide, and the other about 8 m long and rather narrow (2 m high and 1.5 m wide). The ceiling and wall surfaces were irregular, with numerous stalactites and cracks, and rough, crumbling surfaces.

Accounts of Species

Order Insectivora—Insectivores
Family Soricidae—Shrews

Crocidura grayi.—This poorly-known species has been reported previously only

from Luzon and Mindoro (Heaney et al. 1987). A single specimen (with a badly damaged skull) was found dead in 1988 on the road from Summit to Gigmoto, about 4 km E of Summit by road (250 m elevation) in an area of mixed degraded secondary forest and agricultural land.

Order Chiroptera—Bats
Family Pteropodidae—Fruit Bats

Cynopterus brachyotis.—A common, widespread species in Southeast Asia. Most common in disturbed habitat, but present in primary forest (Table 4). In February 1988, nine adult females were multiparous with large nipples but were not lactating; all were pregnant with single embryos (CRL = 3, 5, 7, 8, 10, 14, 15, 18 mm). Four subadults with unfused phalangeal epiphyses had small nipples; two were not pregnant, and two had single embryos of 4 and 5 mm. Five adult males had testes of 3 × 2.5, 4 × 5, 5 × 3, 5 × 4, and 7 × 4; a subadult had testes of 1 × 1.5 mm. Crania are larger than those from Negros and Camiguin, but are nearly identical to a series from Quezon Province (Table 1; Heaney 1984; specimens in UMMZ). Records: Site 1 (2); Site 2 (6); Site 4 (1); Site 5 (5); Site 6 (33).

Eonycteris robusta.—One specimen of this uncommon, poorly known Philippine endemic was captured at Site 2, and two primigravid females were captured at Site 6 on 22 and 24 Feb. 1988; each carried a single embryo (CRL = 3 and 8 mm). Cranial measurements (Table 1) of these specimens fit well within the range of specimens from Luzon and Negros (Heaney & Rabor 1982; specimens in USNM).

Eonycteris spelaea.—A widespread species in Southeast Asia, common in disturbed habitats. One was captured at Site 2 in 1969, and two adult females from Site 6 were pregnant with single embryos of 9 and 12 mm CRL on 22 and 25 February 1988. Cranial measurements (Table 1) are similar to those from Luzon and Negros (Heaney & Rabor 1982; specimens in USNM).

Haplonycteris fischeri.—A Philippine endemic; we found them to be most common in primary forest (Site 5), but present in disturbed forest (Site 6), as is typically the case (Heideman & Heaney 1989). We frequently heard them produce chittering calls in the canopy in the evening at Site 5. In late February 1988, four adult females had large nipples but were not lactating; each carried a single embryo of 3 or 4 mm CRL. Two subadult females had small nipples, and each carried a single embryo of 2 mm CRL. Three adult males had testes 3 × 3, 3 × 3, and 4 × 4 mm. Cranial measurements (Table 1) are similar to those of a series from Luzon, and are slightly larger than those from Dinagat and Negros (Heaney & Rabor 1982; specimens in USNM). Records: Site 4 (5); Site 5 (14); Site 6 (5).

Macroglossus minimus.—A common, widespread species in Southeast Asia. We found them to be most abundant in disturbed habitat (Site 6; Table 1); at both Site 5 and 6 they were taken in or near clumps of wild banana and/or abaca, as is often the case (Heideman and Heaney 1989). In February 1988, two adult females were not pregnant, and six each carried a single embryo of 3, 4, 4, 10, 16, and 22 mm CRL; two were both pregnant and lactating. A single primigravid subadult female had small nipples and a single embryo (CRL = 1 mm). Eight adult males had testes of 6 × 4 to 8 × 7 mm, and six subadults had testes of 1 × 1 to 5 × 3. Cranial measurements (Table 1) are very similar to a series from Negros, but bats from both islands are slightly larger than those from Camiguin and Mindanao (Heaney 1984; specimens in USNM). Records: Site 1 (1); Site 2 (2); Site 5 (1); Site 6 (35).

Ptenochirus jagori.—A common Philippine endemic; in 1988 we found them only at the disturbed forest site (Site 6; Table 1), where they were abundant. Two adult females had large nipples but were not lactating; both carried single embryos of 3 and 4 mm CRL. Two subadult females had small nipples; one was nulliparous, and the other

Table 1.—Means (±SD) and ranges of selected measurements of adult fruit bats (Pteropodidae) from Catanduanes Island, Philippines.

Species	Sex	*n*	Condylobasal length	Zygomatic width	Mastoid width
Cynopterus brachyotis	m	5	27.60 ± 0.49 (27.3–28.3)	18.72 ± 0.55 (18.3–19.6)	11.84 ± 0.22 (11.6–12.0)
Cynopterus brachyotis	f	4	28.23 ± 0.62 (27.6–28.9)	18.85 ± 0.48 (18.4–19.4)	11.95 ± 0.25 (11.7–12.3)
Eonycteris robusta	f	2	32.55 (32.3–32.8)	19.45 (19.3–19.6)	13.90 (13.8–14.0)
Eonycteris spelaea	f	2	33.10 (32.6–33.6)	19.95 (19.8–20.1)	13.35 (13.3–13.4)
Haplonycteris fischeri	m	5	24.16 ± 0.76 (23.2–25.2)	16.42 ± 0.13 (16.2–16.5)	10.70 ± 0.19 (10.4–10.9)
Haplonycteris fischeri	f	5	23.90 ± 0.37 (23.4–24.4)	16.04 ± 0.50 (15.4–16.7)	10.48 ± 0.51 (9.7–11.1)
Macroglossus minimus	m	6	25.23 ± 0.47 (24.4–25.7)	14.78 ± 0.59 (13.7–15.3)	10.05 ± 0.10 (9.9–10.2)
Macroglossus minimus	f	4	25.03 ± 0.46 (24.4–25.5)	13.63 ± 0.42 (13.3–14.1)	9.83 ± 0.19 (9.7–10.1)
Ptenochirus jagori	m	5	34.08 ± 0.69 (33.1–34.6)	24.34 ± 0.91 (22.8–25.1)	14.28 ± 0.22 (14.0–14.6)
Ptenochirus jagori	f	3	33.73 ± 0.40 (33.5–34.2)	23.50 ± 0.79 (22.6–24.1)	14.2 ± 0.0 (14.2)
Pteropus leucopterus	m	1	58.1	33.3	20.5
Rousettus amplexicaudatus	f	1	34.9	20.9	13.9

carried a single embryo of 7 mm CRL. Adult males had testes of 5 × 4 to 7 × 5, and subadults of 2 × 2 and 3 × 2. Cranial measurements (Table 1) are similar to those from central Luzon, and are smaller than those from Camiguin and Negros; adults possess the slightly paler, duller pelage of specimens from Luzon, rather than the darker pelage of those from Negros (Heaney & Rabor 1982, Heaney 1984; specimens in USNM). Records: Site 1 (2); Site 2 (7); Site 4 (2); Site 6 (19).

Pteropus leucopterus.—A rarely captured flying fox endemic to the Philippines, previously known only from Dinagat and Luzon. Two subadult males were netted on a high, denuded ridge at Site 6; both had small testes. Cranial measurements (Table 1) fall within the range reported by Heaney & Rabor (1982).

Pteropus vampyrus.—This widespread Southeast Asian species was reported from Virac by Thomas (1898). Local hunters reported the presence of large flying foxes that could have been this species or *Acerodon jubatus,* or both; they were said to be diminishing in numbers and to be hunted actively.

Rousettus amplexicaudatus.—We captured a single specimen of this common, widespread Southeast Asian species at Site 6; it was a non-pregnant subadult female. A large colony of fruit bats observed but not captured in Cave 1 was probably composed of this species, although they may have been *Eonycteris spelaea.* Cranial measurements

Table 1.—Extended.

Orbital length	Canine to last molar	Molariform toothrow	Palatal breadth	Palatal length	Forearm length
11.50 ± 0.26 (11.2–11.9)	9.46 ± 0.31 (9.1–9.9)	6.72 ± 0.32 (6.3–7.2)	6.18 ± 0.44 (5.7–6.9)	14.10 ± 0.33 (13.6–14.5)	62.4 ± 3.8 (57–66)
11.93 ± 0.36 (11.6–12.4)	9.45 ± 0.21 (9.2–9.7)	6.60 ± 0.08 (6.5–6.7)	6.45 ± 0.35 (6.1–6.8)	14.13 ± 0.55 (13.3–14.4)	65.5 ± 0.6 (56–66)
12.0 (12.0–12.0)	12.35 (12.2–12.5)	8.95 (8.9–9.0)	7.75 (7.6–7.9)	18.00 (17.8–18.2)	73.5 (73–74)
12.15 (11.7–12.6)	11.20 (10.8–11.6)	8.10 (8.1)	7.5 (7.5)	18.05 (17.9–18.2)	71.0 (70–72)
10.22 ± 0.57 (9.6–11.1)	8.56 ± 0.36 (8.1–8.9)	5.90 ± 0.26 (5.6–6.2)	5.06 ± 0.32 (4.6–5.4)	11.62 ± 0.31 (11.3–12.1)	51.0 ± 1.4 (49–52)
9.82 ± 0.43 (9.3–10.4)	8.18 ± 0.22 (8.0–8.5)	5.72 ± 0.19 (5.4–5.9)	5.06 ± 0.40 (4.5–5.6)	11.70 ± 0.37 (11.1–12.0)	50.4 ± 1.5 (48–52)
8.23 ± 0.41 (7.8–8.9)	9.02 ± 0.35 (8.7–9.5)	5.42 ± 0.18 (5.1–5.6)	5.25 ± 0.18 (5.0–5.5)	13.52 ± 0.45 (12.7–13.9)	42.3 ± 1.0 (41–44)
7.90 ± 0.20 (7.8–8.2)	8.73 ± 0.21 (8.5–8.9)	5.50 ± 0.22 (5.3–5.8)	5.10 ± 0.18 (4.9–5.3)	13.63 ± 0.25 (13.3–13.9)	42.8 ± 1.0 (42–44)
15.28 ± 0.68 (14.4–16.0)	12.04 ± 0.21 (11.8–12.3)	8.54 ± 0.25 (8.2–8.9)	7.78 ± 0.43 (7.3–8.4)	17.38 ± 0.35 (16.9–17.8)	82.4 ± 1.7 (80–84)
15.13 ± 0.21 (14.9–15.3)	11.80 ± 0.30 (11.5–12.1)	8.27 ± 0.23 (8.0–8.4)	7.40 ± 0.26 (7.2–7.7)	17.00 ± 0.17 (16.8–17.1)	80.3 ± 0.3 (77–83)
22.0	22.1	16.2	12.4	31.2	134
13.3	13.8	10.7	8.6	18.3	82

fall within the range of series from Luzon, Mindanao, and Negros (Heaney & Rabor 1982, specimens in USNM).

Family Emballonuridae—Sheath-tailed Bats

Emballonura alecto.—We captured a single adult male of this species, which is known from throughout the Philippines, Borneo, and Sulawesi. It was netted in a darkened portion of Cave 1; others were seen high on the walls in moderately-lit portions. Cranial measurements (Table 2) are similar to those from series from Camiguin and Guimaras (Heaney & Rabor 1982, Heaney 1984).

Saccolaimus saccolaimus.—Two specimens were reported from Pandan, Catanduanes by Hollister (1913), and named as a new species (*Taphonycteris capito*). Lawrence (1939) synonymized this taxon with *Taphozous* (*Saccolaimus*) *pluto* Miller (1910; from Mindanao), since both fell within the range of variation of a series from Mindoro. Goodwin (1979) and Koopman (1984) have shown *Saccolaimus saccolaimus* to be a widespread and variable species, and Philippine populations to fall within the range of variation for the species as a whole (specimens in USNM). Lawrence (1939) incorrectly stated that Pandan is in southern Luzon; her error was based on a change in the extent of Albay Province, which included Catanduanes in 1913 but did not in 1939. Cranial measurements (Table 2) fall within the range of specimens from Negros (specimens in USNM).

Table 2.—Means (±SD) and ranges of selected measurements of adult insectivorous bats from Catanduanes Island, Philippines.

Species	Sex	*n*	Condyloincisive length	Zygomatic width	Mastoid width
Emballonura alecto	m	1	13.6	8.5	7.6
Saccolaimus saccolaimus	f	1	22.9	16.0	13.7
Megaderma spasma	m	1	23.1	14.6	11.6
Megaderma spasma	f	1	23.5	14.9	11.5
Hipposideros ater	m	5	14.10 ± 0.19 (13.9–14.1)	7.78 ± 0.05 (7.7–7.8)	8.32 ± 0.11 (8.2–8.4)
Hipposideros ater	f	3	14.50 ± 0.40 (14.1–14.9)	7.83 ± 0.12 (7.7–7.9)	8.40 ± 0.0 (8.4)
Hipposideros diadema	m	3	26.57 ± 0.32 (26.2–26.8)	16.33 ± 0.55 (15.7–16.7)	13.90 ± 0.26 (13.7–14.2)
Hipposideros obscurus	m	1	17.2	10.9	10.1
Hipposideros obscurus	f	1	16.5	10.8	9.5
Rhinolophus arcuatus-s	m	1	18.7	9.6	9.5
Rhinolophus arcuatus-l	m	1	19.5	9.9	10.0
Rhinolophus inops	m	2	21.85 (21.7–22.0)	10.9 (10.9)	10.7 (10.6–10.8)
Rhinolophus inops	f	2	21.65 (21.6–21.7)	10.9 (10.9)	10.4 (10.3–10.5)
Rhinolophus rufus	m	1	28.6	14.6	13.2
Rhinolophus virgo	m	1	15.5	8.5	8.1
Miniopterus australis	m	5	12.80 ± 0.22 (12.5–13.1)	7.30 ± 0.23 (6.9–7.5)	7.36 ± 0.11 (7.2–7.5)
Miniopterus australis	f	5	12.70 ± 0.16 (12.5–12.9)	7.32 ± 0.08 (7.2–7.4)	7.32 ± 0.15 (7.1–7.5)
Miniopterus schreibersii	m	3	15.03 ± 0.21 (14.8–15.2)	8.47 ± 0.16 (8.4–8.6)	8.47 ± 0.15 (8.3–8.6)
Miniopterus schreibersii	f	3	14.66 ± 0.21 (14.5–14.9)	8.33 ± 0.06 (8.3–8.4)	8.17 ± 0.15 (8.0–8.3)
Murina cyclotis	m	1	16.6	10.8	8.9
Scotophilus kuhlii	f	2	17.85 (17.7–18.0)	13.45 (13.0–13.9)	11.75 (11.6–11.9)

Family Megadermatidae—False Vampire Bats

Megaderma spasma.—A widespread species in Southeast Asia. One adult male was netted above a steep slope along the road at Site 6; additionally, one specimen (adult female, 1 embryo, CRL = 11 mm) was netted and several others seen in the main passage of Cave 2. The specimens are slightly larger than two from Mindanao (Heaney & Rabor 1982).

Family Rhinolophidae—Horseshoe-nosed Bats

Hipposideros ater.—A widespread species in Indo-Australia. Thirty to forty individuals were sighted and eleven captured at Cave 2. A few individuals were seen in dimly-lit portions of the main passage, but most were at the end of an entirely dark, narrow side passage. Three adult females were pregnant with single embryos (CRL = 7, 7, 8 mm). The crania are virtually iden-

Table 2.—Extended.

Orbital length	Canine to last molar	Molariform toothrow	Palatal breadth	Palatal length	Forearm length
5.8	5.4	4.1	3.0	5.0	45
9.2	9.6	6.9	6.3	7.0	71.3
7.8	9.0	6.9	3.9	7.2	59
7.8	9.1	7.2	3.7	7.2	63
4.94 ± 0.09 (4.9–5.1)	4.86 ± 0.05 (4.8–4.9)	3.96 ± 0.15 (3.8–4.2)	3.22 ± 0.15 (3.0–3.4)	4.98 ± 0.15 (4.8–5.2)	40.8 ± 0.4 (40–41)
5.00 ± 0.10 (4.9–5.1)	4.93 ± 0.15 (4.8–5.1)	3.97 ± 0.06 (3.9–4.0)	3.23 ± 0.06 (3.2–3.3)	5.10 ± 0.10 (5.0–5.2)	42.0 ± 1.0 (41–43)
9.73 ± 0.45 (9.3–10.2)	10.67 ± 0.15 (10.5–10.8)	8.23 ± 0.30 (7.9–8.5)	7.17 ± 0.15 (7.0–7.3)	10.47 ± 0.31 (10.2–10.8)	—
6.9	6.6	5.7	5.2	6.2	48
6.5	6.5	5.1	5.2	6.2	47
5.4	7.5	5.5	4.0	6.3	45
5.6	8.0	5.9	3.9	6.5	47
6.25 (6.2–6.3)	8.85 (8.8–8.9)	6.45 (6.4–6.5)	4.50 (4.5)	7.65 (7.5–7.8)	51.0 (49–53)
6.10 (6.0–6.2)	8.90 (8.8–9.0)	6.60 (6.6)	4.70 (4.6–4.8)	7.55 (7.4–7.7)	50.5 (50–51)
7.9	11.9	8.9	6.5	10.7	68
4.8	6.2	4.6	3.6	5.6	43
4.22 ± 0.22 (3.9–4.5)	5.08 ± 0.08 (5.0–5.2)	3.70 ± 0.10 (3.6–3.8)	2.94 ± 0.05 (2.9–3.0)	5.94 ± 0.32 (5.5–6.2)	36.0 ± 0.7 (35–37)
4.12 ± 0.13 (3.9–4.2)	5.12 ± 0.08 (5.0–5.2)	3.70 ± 0.0 (3.7)	2.84 ± 0.09 (2.7–2.9)	5.52 ± 0.08 (5.4–5.6)	36.2 ± 0.4 (36–37)
5.30 ± 0.17 (5.2–5.5)	6.23 ± 0.06 (6.2–6.3)	4.47 ± 0.06 (4.4–4.5)	3.53 ± 0.06 (3.5–3.6)	6.70 ± 0.26 (6.4–6.9)	44.7 ± 0.6 (44–45)
5.13 ± 0.12 (5.0–5.2)	6.07 ± 0.12 (6.0–6.2)	4.33 ± 0.06 (4.3–4.4)	3.43 ± 0.06 (3.4–3.5)	6.47 ± 0.21 (6.3–6.7)	43.5 (43–44)
6.0	6.0	4.9	3.7	7.7	—
7.0 (7.0)	6.80 (6.8)	5.40 (5.4)	5.00 (4.8–5.2)	7.85 (7.7–8.0)	50.2 (49.0–52.0)

tical to a series from Luzon (specimens in USNM).

Hipposideros diadema.—A common species, widespread in Indo-Australia. Three specimens in the USNM from Baras and Pandan were reported by Hollister (1913); we captured none.

Hipposideros obscurus.—A poorly-known Philippine endemic species previously known only from Dinagat, Luzon, and Mindanao. We captured two individuals at Site 5, an adult female (not pregnant) in a mist net on a low ridge in primary forest and an adult male that we saw roosting at the closed end of a hollow in a log less than 50 m from the netting site. The log was ca. 10 m long and from 1.0 to 1.6 m in diameter, and the hollow 6 m long and 0.4 to 0.6 m in diameter; dim light penetrated to the roosting site. Cranial measurements are slightly larger than those of one specimen from Dinagat (Heaney & Rabor 1982) and identical to a series from Luzon (in USNM).

Rhinolophus arcuatus.—Studies current-

ly in progress indicate that two very similar species that are present in the Philippines have been reported under this name: a slightly smaller species (designated "*R. arcuatus*-s" in Table 2) that is associated with lowland caves and a slightly larger species ("*R. arcuatus-l*") that is associated with upland primary forest. J. E. Hill (in litt.) has suggested that these are *R. arcuatus* and *R. anderseni,* but we have not examined the holotype of *R. anderseni* in Madrid, and so identification remains uncertain. We captured an adult male of the larger species in a ridge-top clearing at Site 6, and an adult male of the smaller species in Cave 1 in a very dimly-lit portion of the main passage. Cranial measurements (Table 2) for each are typical of larger series from Negros (specimens in USNM).

Rhinolophus inops.—A poorly known Philippine endemic, previously reported only from Luzon, Mindanao, Mindoro, and Negros (Heaney et al. 1987; specimens in USNM). We captured six and saw many more in the main passage of Cave 1. One adult female was pregnant with a single embryo (CRL = 3 mm); the other was not pregnant. Four adult males had testes of 1 × 1 or 1 × 2. Cranial measurements (Table 2) fall within the range of those from Luzon and Negros (specimens in USNM).

Rhinolophus rufus.—A single specimen of this poorly known Philippine endemic was captured and several others seen in 1988 in a shallow rock overhang along a small river that is about 8 km W Gigmoto.

Rhinolophus virgo.—An endemic species widespread within the Philippines. We netted a single adult male on a low ridge in primary forest at Site 5.

Family Vespertilionidae—Common Bats

Miniopterus australis.—Both this and the following species are widespread in Indo-Australia. We netted 32 *M. australis* and 7 *M. schreibersii* from a colony of several hundred *Miniopterus* in a very dim portion of the main passage of Cave 1; many were roosting in small groups (from one to five) inside small solution holes in the ceiling. All females were adults; all had tiny uteri and none were lactating. The adult males had tiny testes.

Miniopterus schreibersii.—In addition to the seven netted at Cave 1, we captured one *M. schreibersii* along the road above the river at Site 6. Three adult females had tiny uteri and were not lactating; five adult males had testes of 1 × 1 mm or less.

Murina cyclotis.—Widespread in Southern Asia; known previously in the Philippines from single specimens from Luzon and Mindanao (Heaney et al. 1987). We netted one adult male along the edge of the road above a steep drop to the river at Site 5.

Scotophilus kuhlii.—Three specimens in the USNM of this common, widespread commensal species from Pandan were reported by Hollister (1913); we captured none, but saw several bats flying over Virac that probably were this species.

Order Primates
Family Cercopithecidae—Monkeys

Macaca fascicularis.—PCG saw monkeys on a number of occasions in 1968–1971 at localities scattered around Catanduanes, and considered them to be moderately common. In 1988, hunters reported their presence to us, but said that they had declined and were absent from many parts of the island. No specimens are available.

Order Rodentia
Family Muridae—Rats and Mice

Apomys microdon.—A very poorly known species (Musser 1982), recently taken on Mt. Isarog in southern Luzon (Rickart et al. 1991). The single specimen, the holotype of the species, is from Biga (=Viga; Hollister 1913); we captured none. No information on the habitat or mode of acquisition of this specimen is on file at the USNM.

Phloeomys cumingi.—A very poorly known species previously reported only from southern Luzon and Marinduque. This giant arboreal rat was said by local hunters and farmers to be fairly common in 1988, and they obtained 13 specimens for us. These were captured in a hilly area that is a mosaic of degraded forest on steep slopes and agricultural land on less steep slopes; much of the cleared land consists of old, heavily vegetated patches of abaca and coconut and scattered tall trees. All were found by dogs in hollow logs or live hollow trees; they were driven out with smoke and fire and captured either by the dogs or by hand. Several of the standing trees were described as slanted; all were at least 40 cm in diameter.

Local hunters and farmers reported these animals to be strictly nocturnal and principally arboreal, always to nest in hollow trees, to have one young at a time and typically one young per year, and usually to live singly or in pairs (mother and offspring or adult male and female) although larger groupings had been seen. They were said to feed on tender young leaves of trees (especially red, flushing leaves), not to damage crops, and to be hunted occasionally for their meat.

Of two adult males obtained in February 1988, neither (1.74 and 1.95 kg) appeared to be in breeding condition; testes of one were 15 × 10 mm. One young adult male (1.45 kg) had testes 8 × 5 mm. Two nulliparous subadult females weighed 1.14 and 1.15 kg. Adult females (n = 6) ranged in weight from 1.45 to 2.1 kg; two had single nursing young that weighed 480 and 665 g, and each had a single discernable uterine scar. Four adult females had no uterine scars and were not lactating. These data indicate that births take place during the late rainy season (roughly December). The lack of reproductive activity in middle to late February (other than lactation) suggests that there is a lull in breeding activity at least during the dry season (late January to May, and perhaps early rainy season (June to August) as well.

Cranial measurements (Table 3) are slightly smaller than those of a series from Mt. Isarog, southern Luzon, and much smaller than those of *P. pallidus* from central and northern Luzon (specimens in USNM). Pelage of all specimens was entirely dark brown, as is typical for this species, rather than the pale gray and dark brown of *P. pallidus.*

Rattus everetti.—We trapped this common but ecologically poorly-known Philippine endemic at Site 3 in 1969, and at Sites 5 and 6 in 1988. Most individuals at Site 5 were trapped adjacent to or beneath logs or at the base of trees, nearly always where there was cover from the logs or leafy vegetation. At Site 6, we caught these rats in both remnant forest and in heavily disturbed agricultural areas. At both sites animals were caught most often in steep areas, and rarely on flat ground except where there were fallen logs. One released rat initially hid on the ground in a tangle of vines and dead leaves; when chased it ran quickly and easily up the trunk of a large tree. One animal was caught during daylight hours, and all others at dusk or after dark.

Three subadult males with abdominal testes taken in February 1988 weighed 190–230 g; testes were 12 × 6 mm or smaller. Males with scrotal testes (n = 17) weighed 230–420 g; testis size ranged from 19 × 11 mm to 45 × 17 mm. Nulliparous females (n = 15) weighed from 110 to 270 g. No females with embryos were captured. Females with placental scars weighed 245–350 g; three apparently primigravid females (245, 260, 285 g) had 3, 5, and 10 scars, respectively. Multiparous females (n = 8) weighed 280 g or more, and retained several sets of uterine scars so that counts were not possible (one showed at least 18 scars). Records: Site 3 (7); Site 5 (45); Site 6 (8).

Rattus exulans.—Hollister (1913) described *Rattus leucophaetus* (now considered a synonym of *Rattus exulans*; Musser

Table 3.—Means (±SD) and ranges of selected measurements of adult murid rodents from Catanduanes Island, Philippines. Values in brackets were taken by LRH on dried skins.

Species	Sex	*n*	Condylobasal lenth	Zygomatic width	Mastoid width	Rostral length
Apomys microdon	?	1	—	—	—	—
Phloemys cumingi	m	2	77.68 (75.3–80.0)	40.30 (39.3–41.3)	23.55 (23.5–26.5)	32.90 (31.6–34.2)
Phloemys cumingi	f	3	75.27 ± 3.72 (27.2–79.4)	40.23 ± 1.36 (38.8–41.5)	22.73 ± 0.92 (22.2–23.8)	32.23 ± 1.56 (30.8–33.9)
Rattus everetti	m	9	50.39 ± 2.99 (47.0–57.1)	25.53 ± 1.44 (23.5–28.1)	18.58 ± 0.30 (18.2–19.1)	20.50 ± 1.41 (18.7–23.3)
Rattus everetti	f	7	48.87 ± 2.22 (45.9–52.0)	24.15 ± 0.79 (23.4–25.1)	17.75 ± 0.64 (17.0–18.6)	20.06 ± 1.14 (18.3–21.7)
Rattus exulans	f	1	27.3	14.3	12.3	10.0

1977) on the basis of a single specimen from Bagamanoc, Catanduanes. We trapped a single specimen of this widespread commensal species in scrubby second-growth forest along the riverbank at Site 6.

Rattus rattus.—Hollister (1913) reported three specimens of this abundant commensal from Bagamanoc, Catanduanes; the USNM also contains specimens from Baras (1), Calolbon (2), Caramoran (1), Gigmoto (1), Pandan (2), and Viga (1). Six specimens were trapped at Site 3 in the same trap lines where 7 *R. everetti* were taken. We trapped a single adult male in primary forest at Site 5, in a trap under a small log at the base of a large tree; the same trap later captured a *Rattus everetti.*

Order Carnivora
Family Viverridae—Civets

Paradoxurus hermaphroditus and *Viverra tangalunga.*—PCG saw a captive *Viverra tangalunga* near Site 2 in 1969. He also saw an animal at dusk, near Kangkoyawe in 1968, that he believed to be *Paradoxurus hermaphroditus.* In 1988, local hunters and farmers from the vicinity of Site 6 described these two species of small carnivores to us, giving sufficient details that we are confident of their identities. Both were said to be moderately common. No specimens are available.

Order Artiodactyla
Family Suidae—Pigs

Sus barbatus.—PCG heard numerous reports of successful pig hunts from 1968 to 1971, and saw tracks and areas where pigs had rooted in the forest floor. In 1988, hunters and farmers reported the presence of wild pigs, but said that they were heavily hunted and restricted generally to a few inaccessible areas of the island. No specimens are available.

Family Cervidae—Deer

Cervus mariannus.—PCG saw an adult male Philippine brown deer that had been shot near Dugui-too in 1968, and heard of other successful hunts in other areas. In 1988, hunters and farmers reported deer to be nearly extinct on the island; no one we talked with knew of any being captured in the last few years. No specimens are available.

Results and Discussion

To summarize the critical points of the description of Catanduanes given above: (1) there was a land-bridge connection to Luzon in the recent past; (2) the island is rather small in total area; and (3) the vegetation was originally predominantly lowland dipterocarp forest. These points and the dis-

Table 3.—Extended.

Orbital length	Molariform toothrow	Palatal breadth	Diastema length	Head & body length	Tail length
	5.4	5.5	6.6	[103]	[136]
25.00	17.25	16.75	22.70	385.5	—
(24.5–25.5)	(17.2–17.3)	(16.3–17.2)	(22.4–23.0)	(370–401)	—
24.60 ± 0.85	17.90 ± 0.70	16.40 ± 0.17	21.43 ± 1.01	352.3 ± 30.4	327.0 ± 4.2
(23.7–25.4)	(17.1–18.4)	(16.2–16.5)	(20.8–22.6)	(330–387)	(324–330)
18.43 ± 0.79	9.23 ± 0.41	9.37 ± 0.23	14.37 ± 1.21	239.2 ± 12.9	244.3 ± 9.4
(17.4–20.0)	(8.7–9.8)	(9.1–9.7)	(13.0–17.0)	(222–260)	(234–257)
17.96 ± 0.63	9.31 ± 0.30	9.30 ± 0.43	14.00 ± 0.82	225.0 ± 15.5	229.4 ± 7.0
(17.1–18.4)	(8.9–9.7)	(8.5–9.8)	(12.7–15.1)	(203–242)	(222–242)
10.3	5.1	5.9	6.9	[118]	[108]

cussion and predictions in Heaney (1986), Heaney et al. (1989), and Heaney (1991) led us to predict (before visiting the island in 1988) that the island should be characterized by 1) a mammalian fauna shared entirely with Luzon, 2) species richness lower than that of Luzon, with species richness of non-volant mammals falling on or near the species richness/area curve for the Mindanao faunal region, 3) the species richness of fruit bats falling on the species richness/area curve for other fruit bat faunas in the Philippines, and 4) a fauna composed of species found at low to moderate elevations on Luzon.

Adequacy of sampling.—Before considering the data collected, it is important to consider the likelihood that current information reflects the total mammalian species richness of Catanduanes. We believe that there are five principal habitats that need to be sampled on any given Philippine island in order to assess the fauna: lowland forest, montane forest, mossy forest, second growth, and caves (Heaney et al. 1989, Rickart et al. 1991). We judge current trapping and netting samples from lowland forest to be minimally acceptable. Recent studies in the Philippines have shown that our 1988 samples of 100 fruit bats from primary forest and forest/clearing mosaic locality are likely to approximate species richness and proportional abundance, although rare species may be missed (Heideman & Heaney 1989). Similarly, trapping samples based on 900 traps-nights are adequate to document species richness and rough proportional abundance, but again rare species may be missed (Heaney et al. 1989, Rickart et al. 1991). In both cases, important prior records supplement these lists. Thus, our lowland forest samples probably include most fruit bats and small non-volant mammals that are present, but a few gaps may remain.

No reliable estimates of Philippine microchiropteran faunas are available, and so no comparisons are possible. However, with 15 species recorded, Catanduanes has one of the richer known faunas.

Our samples from caves and second growth are less extensive, and are unlikely to be complete; more sampling is needed.

Most importantly, we were unable to sample either montane or mossy forest. Although Catanduanes has a maximum elevation of 764 m, which is below the lower limits of montane and mossy forest on large mountains (1000 m and 1500 m, respectively; Heaney et al. 1989, Rickart et al. 1991), we have found montane forest as low as 650 m and mossy forest as low as 900 m on Leyte (Heaney et al. 1989), and believe both may be present on Catanduanes as isolated fragments. Although bats tend to be rare in both habitats, at least one species (*Harpyionycteris whiteheadi*) occurs pri-

Table 4.—Numbers of fruit bats (Pteropodidae) captured in mist nets in primary forest (Site 5) and mixed disturbed forest and agricultural clearings (Site 6) on Catanduanes Island in 1988. The number of captures per net-night are given in parentheses. See text for site descriptions.

	Site 5	Site 6
Cynopterus brachyotis	5 (0.08)	33 (0.75)
Eonycteris robusta	0	2 (0.05)
Eonycteris spelaea	0	2 (0.05)
Haplonycteris fischeri	14 (0.21)	5 (0.11)
Macroglossus minimus	1 (0.15)	35 (0.78)
Ptenochirus jagori	0	19 (0.43)
*Pteropus leucopterus**	0	2 (0.05)
Rousettus amplexicaudatus	0	1 (0.02)
Total fruit bats	20	99
Total net-nights	66	44
Fruit bats/net-night	0.30	2.25
Fruit bat species	3	8
Standardized total	20	97
Standardized bats/ net-night	0.30	2.20
Standardized species richness	3	7

* = Species excluded from standardized total to allow comparison to data from other islands.

marily in upland forest (Heaney et al. 1989), and rodents and shrews typically increase in diversity and abundance with increasing elevation (Rickart et al. 1991). It is almost certain that sampling of such habitats would add species to the current list.

Netting and trapping success.—We captured 119 fruit bats of eight species and seven insectivorous bats of six species in 110 net-nights at our forest sites in 1988. These samples for fruit bats are large enough for comparison with other sites in the Philippines. Standardized netting success (see methods) for fruit bats (Table 4) at the 1988 disturbed site (Site 6) was over seven times that in primary forest (Site 5; 0.3 vs. 2.2 bats per net-night); this difference is typical for disturbed vs. undisturbed sites on Negros and Leyte (Heaney et al. 1989). However, netting success was less than one-third that in comparable vegetation on Negros and Leyte. Proportionate composition of the fruit bat communities differed significantly at the two sites (G-test, $G = 47.2$, $df = 7$, $P < 0.005$), with *Haplonycteris fischeri* most common in primary forest (Site 5) and *Cynopterus brachyotis, Macroglossus minimus,* and *Ptenochirus jagori* most common in disturbed habitat (Site 6). *Cynopterus brachyotis, Eonycteris spelaea, M. minimus,* and *Rousettus amplexicaudatus* typically are associated with moderately to heavily disturbed habitat in the Philippines, whereas *P. jagori* is a primary forest species that is most strongly associated with clearings in primary forest and lightly disturbed forest (Heaney et al. 1989, Heideman & Heaney 1989).

We captured 55 small mammals of three species in 1010 trap-nights during 1988. Trap success in primary forest (Site 5; 45 *Rattus everetti* and 1 *Rattus rattus* in 890 trap-nights) was 5.2/100 trap-nights, and in secondary forest (Site 6; 8 *R. everetti* and 1 *Rattus exulans* in 120 trap-nights) was 7.5/100 trap-nights; this is higher than in comparable habitat on Leyte or Negros by about a factor of 2. Species richness was quite low, which is typical of low elevation forest in the Philippines (Heaney et al. 1989, Rickart et al. 1991).

We captured eight species of insectivorous bats in caves and rock shelters (*Megaderma spasma, Emballonura alecto, Rhinolophus cf. arcuatus, R. inops, R. rufus, Hipposideros ater, Miniopterus australis,* and *M. schreibersii*) and observed one species of fruit bat (probably *Rousettus amplexicaudatus*; see species account). The cave fauna is generally similar to that found previously in Philippine caves (Taylor 1934, Lawrence 1939, Sanborn 1952), although no basis for quantitative comparison is available.

Biogeography.—Of the 35 species of mammals now recorded from Catanduanes, all but one are also known from neighboring Luzon. The one exception is *Saccolaimus saccolaimus,* a species that occurs from India to the Solomon Islands, and within the Philippines is known from Catanduanes, Mindanao, Mindoro, and Negros (Heaney

et al. 1987). The small number of specimens and their scattered occurrence suggest that this species is poorly sampled in the Philippines and might occur on Luzon. The presence of the remaining 34 species on Luzon is supportive of prediction 1 given above.

Only one species known from Catanduanes, *Phloeomys cumingi,* is restricted to Luzon and associated small islands. Approximately 18 additional murid rodents and one fruit bat are endemic to Luzon but are not known from Catanduanes. However, *Crocidura grayi* is restricted to Luzon and Mindoro, and preliminary studies by Heaney indicate that the mouse *Apomys microdon* may be restricted to Catanduanes and southern Luzon. Thus, although most of the mammalian fauna of Catanduanes is composed of widespread species, several species are specifically indicative of its past association with southern Luzon.

With 10 known species of non-volant mammals (eight of which are indigenous), Catanduanes clearly has a smaller fauna than Luzon, which has at least 35 (28 of which are indigenous; Heaney 1986). An island the size of Catanduanes in the Mindanao island group is expected to have about 12 indigenous species. Prediction 2 is thus supported only to the extent that the fauna is smaller than that of Luzon; it is also smaller than expected on the basis of islands in the Mindanao faunal region. Sampling of upland habitats is needed to determine the adequacy of current data.

Prediction 3 is supported by our findings: the nine species of fruit bats fall within the 95% confidence limits for other Philippine faunas (Heaney 1991). However, this is two species fewer than the predicted eleven species, and we suspect that other species (especially of *Pteropus*) remain to be discovered on Catanduanes.

Prediction 4 can be tested only partially with current data. Nearly all species known from Catanduanes are also found in lowland habitats on nearby Mt. Isarog on Luzon (Rickart et al. 1991; specimens in USNM), and the upland rodents known from Mt. Isarog are absent; both observations support the prediction. However, some upland rodents might be present but currently unsampled, as noted above.

Comparison with birds.—The avifauna of Catanduanes is among the best-known of any on small islands in the Philippines (Gonzales 1983; Goodman & Gonzales 1989; Manuel 1937). The birds show biogeographic patterns that are strikingly similar to those of mammals. The avifauna of 146 species is entirely composed of species also found on Luzon, which has about 195 species (Hauge et al. 1986). With the exception of the endemic subspecies *Gallicolumba luzonica rubiventris,* a ground dove, all other reported subspecies on Catanduanes are also found on Luzon. The number of resident bird species in lowland forest and parang (anthropogenic grassland) on Catanduanes is 108, compared to 111 species in comparable habitat on Mt. Isarog, a relatively well-known mountain on the adjacent mainland of Luzon (Goodman and Gonzales 1990:33). However, of nine species (*Otus longicornis, Napothera rabori, Stachyris whiteheadi, Turdus poliocephalus, Brachypteryx montana, Ficedula hyperythra, Ficedula westermanni, Phylloscopus trivirgatus, Aethopyga pulcherrima*) associated with montane and mossy forest on Mt. Isarog, none are known from Catanduanes.

The avifauna thus conforms to the predictions presented above for the mammal fauna: it is shared entirely with Luzon, species richness is lower than that of Luzon, and it is composed of an attenuated portion of the fauna associated with lowland habitats on Luzon, with no obligate upland species. Because no analysis of species/area relationships has yet been carried out for birds in the Philippines, no quantification of this variable is possible. Nevertheless, the concordance of general patterns between these vertebrate groups is high. Further, more detailed comparisons are warranted.

Conclusion

Although still incompletely known, the mammal fauna of Catanduanes is clearly similar to that of adjacent Luzon, with no evidence of endemic species or representatives of other regions of the Philippines; in these ways it conforms to expectations for an island of its location and geological history. All predictions based on prior studies in the Philippines are supported, but the data are generally indicative of a smaller fauna than anticipated. Further field inventories of high elevation habitats are necessary to fully test predictions regarding the species richness and biogeographic origin of the fauna.

Acknowledgments

We thank A. Batal, R. Fernandez, S. M. Goodman, J. Ramos, D. A. Samson, and L. Tagat for energetic assistance with the field work, and L. Basmayor of Bicol State University for logistical assistance. The manuscript has benefited from editorial comments from M. D. Carleton, S. M. Goodman, P. D. Heideman, S. M. G. Hoffman, D. Klingener, and C. B. Robbins. We also thank L. Gordon and D. Schmidt for technical assistance. This research was supported by the National Science Foundation (BSR-8514223), the Smithsonian Institution Office of Fellowships and Grants, and the Philippine National Museum.

Literature Cited

Case, T. J., & M. L. Cody. 1983. Island biogeography in the Sea of Cortez. University of California Press, Berkeley, 508 pp.

Gonzales, P. C. 1983. Birds of Catanduanes.—Zoological Papers National Museum Manila No. 2: 1–125.

Goodman, S. M., & P. C. Gonzales. 1989. Notes on Philippine birds, 12. Seven species new to Catanduanes Island.—Bulletin of the British Ornithological Club 109:48–50.

———, & ———. 1990. The birds of Mt. Isarog National Park, southern Luzon, Philippines, with particular reference to altitudinal distribution.—Fieldiana Zoology 1414:1–39.

Goodwin, R. E. 1979. The bats of Timor: systematics and ecology.—Bulletin of the American Museum of Natural History 163:73–122.

Hamilton, W. 1979. Tectonics of the Indonesian region.—Geological Survey Professional Papers 1078:1–345.

Hashimoto, W. 1981. Geological development of the Philippines. Pp. 83–170, and Supplementary notes on the geological history of the Philippines by Hashimoto. Pp. 171–192 *in* T. Kobiyashi, R. Toriyama, & W. Hashimoto, eds., Geology and palaeontology of Southeast Asia 22:1–192.

Hauge, P., J. Terborgh, B. Winter, & J. Parkinson. 1986. Conservation priorities in the Philippines—Forktail 2:83–91.

Heaney, L. R. 1984. Mammals from Camiguin Island, Philippines.—Proceedings of the Biological Society of Washington 97:119–125.

———. 1986. Biogeography of mammals in Southeast Asia: estimates of rates of colonization, extinction, and speciation.—Biological Journal of the Linnean Society 28:127–165.

———. 1991. An analysis of patterns of distribution and species richness among Philippine fruit bats (Pteropodidae).—Bulletin of the American Museum of Natural History (in press).

———., P. D. Gonzales, & A. C. Alcala. 1987. An annotated checklist of the taxonomic and conservation status of land mammals in the Philippines.—Silliman Journal 34:32–66.

———, P. D. Heideman, E. A. Rickart, R. B. Utzurrum, & H. Klompen. 1989. Elevational zonation of mammals in the central Philippines.—Journal of Tropical Ecology 5:259–280.

———, & B. D. Patterson (eds.) 1986. Island biogeography of mammals.—Biological Journal of the Linnean Society 28:1–271.

———, & D. S. Rabor. 1982. Mammals of Dinagat and Siargao islands, Philippines.—Occasional Papers of the Museum of Zoology, University of Michigan 699:1–30.

Heideman, P. D., & L. R. Heaney. 1989. Population biology and estimates of abundance of fruit bats (Pteropodidae) in Philippine submontane rainforest.—Journal of Zoology (London) 218:565–586.

Hollister, N. 1913. A review of the Philippine land mammals in the United States National Museum.—Proceedings of the United States National Museum 46:299–341.

Koopman, K. F. 1984. Taxonomic and distributional notes on tropical Australian bats.—American Museum Novitates 2778:1–48.

Lawrence, B. 1939. Collections from the Philippines. Mammals.—Bulletin of the Museum of Comparative Zoology, Harvard University 86:38–73.

Manalo, E. B. 1956. The distribution of rainfall in the Philippines.—Philippine Geographical Journal 4:104–166.

Manuel, C. G. 1937. Avifauna of Catanduanes.—Philippine Journal of Science 63:185–189.

Miller, G. S. 1910. Descriptions of two new genera and sixteen new species of mammals from the Philippine Islands.—Proceedings of the United States National Museum 38:391–404.

Musser, G. G. 1977. *Epimys benguetensis,* a composite, and one zoogeographic view of rat and mouse faunas in the Philippines and Celebes.—American Museum Novitates 2624:1–15.

———. 1982. Results of the Archbold Expeditions. No. 108. The definition of the genus *Apomys,* a native rat of the Philippine Islands.—American Museum Novitates 2746:1–43.

Philippine Bureau of Mines. 1963. Geological map of the Philippines. Bureau of Mines, Manila.

Rickart, E. A., L. R. Heaney, & R. B. Utzurrum. 1991. Distribution and ecology of small mammals along an elevational transect in southeastern Luzon, Philippines.—Journal of Mammalogy (in press).

Sanborn, C. C. 1952. Philippine zoological expedition 1946–1947. Mammals.—Fieldiana: Zoology 33:89–158.

Taylor, E. H. 1934. Philippine land mammals.—Monographs of the Bureau of Science (Manila) 30:1–548.

Thomas, O. 1898. On the mammals obtained by Mr. John Whitehead during his recent expedition to the Philippines.—Transactions of the Zoological Society of London 14 (6):377–414.

Whitmore, T. C. 1984. Tropical rain forests of the Far East. Clarendon Press, Oxford, 352 pp.

(LRH) Division of Mammals, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605; (PCG) Zoology Section, Philippine National Museum, Rizal Park, Manila, Philippines; (RCBU) Department of Biology, Silliman University, 6200 Dumaguete City, Negros Oriental, Philippines (current address: Department of Biology, Boston University, 5 Cummington Street, Boston, Massachusetts 02215); (EAR) Utah Museum of Natural History, University of Utah, Salt Lake City, Utah 84112.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

% British Museum (Natural History)
Cromwell Road
London SW7 5BD
01-938 9387

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 20 December 1990 in Vol. 47, Part 4 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD.

Case No.

2768 *Lepidomenia* Kowalevsky in Brock, 1883 (Mollusca, Solenogastres): proposed designation of *Lepidomenia hystrix* Marion & Kowalevsky in Fischer, 1885 as the type species.

2739 *Helicarion* Férussac, 1821 (Mollusca, Gastropoda): proposed conservation, and proposed designation of *Helixarion cuvieri* Férussac, 1821 as the type species.

2588 *Haminaea* Leach, [1820] (Mollusca, Gastropoda): proposed conservation.

2670 *Kobeltia* Seibert, 1873 (Mollusca, Gastropoda): proposed confirmation of *Arion hortensis* Férussac, 1819 as the type species.

2747 *Strophomena* de Blainville, 1825 (Brachiopoda): proposed designation of *Leptaena planumbona* Hall, 1847 as the type species.

2703 HOMALOPTERIDAE Bleeker, 1859 (Osteichthyes, Cypriniformes): proposed precedence over BALITORIDAE Swainson, 1839.

2715 *Lepomis* Rafinesque, 1819 (Osteichthyes, Perciformes): proposed fixation of masculine gender for the name.

2141 *Rana sphenocephala* Cope, 1886 (Amphibia, Anura): proposed precedence over *Rana utricularius* Harlan, 1826.

Opinion published in the *Bulletin of Zoological Nomenclature*

The following Opinion was published on 20 December 1990 in Vol. 47, Part 4 of the *Bulletin of Zoological Nomenclature*:

Opinion 1622. *Heliastes ovalis* Steindachner, 1900 (currently *Chromis ovalis*; Osteichthyes, Perciformes) specific name conserved

REVIEWERS

The following people reviewed manuscripts for the *Proceedings* in 1990. P. Alderslade, K. Anderson, W. D. Anderson, Jr., H. Andres, K. Baba, C. C. Baldwin, R. Bamber, R. C. Banks, R. Birdsong, J. Blake, J. P. Bogart, R. W. Bouchard, T. E. Bowman, G. Boxshall, P. Brazaitis, C. de Broyer, A. J. Bruce, N. L. Bruce, R. C. Brusca, P. A. Buckup, S. D. Cairns, C. B. Calloway, E. Campos, D. Cannatella, M. D. Carleton, K. E. Carpenter, F. A. Chace, Jr., J. Chess, J. Clark, E. Coan, R. F. Cressey, M. M. Criales, A. Crosnier, D. Danielipol, G. M. Davis, P. Delaney, D. Dlingener, M. Dojiri, W. E. Duellman, E. Escobar-Briones, K. Fauchald, D. G. Fautin, R. M. Feldman, F. D. Ferrari, S. V. Fink, W. L. Fink, J. F. Fitzpatrick, Jr., R. Franz, G. Fryer, A. L. Gardner, J. S. Garth, M. Grasshoff, R. B. Griffis, H. Griffith, E. Harada, M. G. Harasewych, S. C. Harris, L. R. Heaney, R. W. Heard, J. W. Hedgpeth, G. F. Hevel, R. W. Heyer, R. P. Higgins, A. Hirayama, J. -s. Ho, G. J. Howes, P. Hutchins, K. Izawa, K. Jazdzewski, G. D. Johnson, J. Just, Z. Kabata, B. Kensley, T. Kikuchi, K. F. Koopman, F. Krapp, K. Kuroda, S. Lanyon, D. Laubitz, M. Ledoyer, R. Lemaitre, R. B. Manning, R. H. Mapes, R. N. Mariscal, J. W. Martin, W. N. Mathis, J. E. McCosker, R. W. McDiarmid, L. McKinney, D. McKinnon, P. A. McLaughlin, J. H. McLean, J. McLelland, M. Milligan, T. Miura, R. F. Modlin, R. Mooi, R. Moore, P. Mundel, G. Musser, A. Myers, D. Nelson, P. K. L. Ng, N. Ngoc-Ho, P. E. Olsen, S. L. Olson, J. M. Orensanz, C. Ostman, D. L. Pawson, L. H. Pequegnat, P. D. Perkins, M. H. Pettibone, J. Pojeta, G. C. B. Poore, W. L. Pratt, A. J. Provenzano, G. E. Ramos, J. E. Randall, P. Rasmussen, M. J. Reaka, A. L. Rice, C. B. Robbins, H. W. Robison, G. Rodriquez, D. E. Russell, R. D. Sage, M. de Saint Laurent, K. Sakai, S. A. Schaeffer, D. Schmidly, R. Sluys, A. E. Smalley, D. F. Soule, P. J. Spangler, H. J. Squires, D. W. Steadman, D. J. Stewart, G. C. Steyskal, D. Sues, I. Takeuchi, M. Thurston, N. M. Tirmizi, P. Tucker, E. Van der Straeten, R. W. M. van Soest, R. P. Vari, J. C. von Vaupel Klein, W. N. Verheyen, J.-W. Wagele, L. A. Ward, L. Watling, B. Werding, M. J. Wetzel, M. K. Wicksten, A. B. Williams, J. T. Williams, J. Winston, W. W. Wirth, E. L. Yochelson, H. Zibrowius, W. Ziedler.

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON" a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Apendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

Proofs.—Authors will receive first proofs and original manuscript for correction and approval. Both must be returned within 48 hours to the Editor. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, **changes in proofs ($3.00 per change or revision),** and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

CONTENTS

New records of Stylasteridae (Hydrozoa: Hydroida) from the Galápagos and Cocos Islands
Stephen D. Cairns 209
Monocelididae (Platyhelminthes: Proseriata) from Puerto Rico. I. Genera *Minona* and *Monocelis*
Marco C. Curini-Galletti 229
Arene boucheti, a new intertidal liotiine turbinid (Mollusca: Gastropoda: Trochoidea) from Trindade Island, South Atlantic Ocean
José H. Leal 241
Annina fustis, a new isopod from Phang Nga, Thailand (Crustacea: Isopoda: Cirolanidae)
Thomas E. Bowman and Thomas M. Iliffe 247
Revision of Iphimediidae and similar families (Amphipoda: Gammaridea)
C. O. Coleman and J. L. Barnard 253
Curidia magellanica, new species, from Magellan Strait (Crustacea: Amphipoda: Ochlesidae)
C. O. Coleman and J. L. Barnard 269
Amatiguakius forsberghi, a new genus and species from Alaska (marine Amphipoda: Epimeriidae)
C. O. Coleman and J. L. Barnard 279
A new genus and two new species of freshwater crabs from México, *Odontothelphusa toninae* and *Stygothelphusa lopezformenti* (Crustacea: Brachyura: Pseudothelphusidae)
Fernando Alvarez and José Luis Villalobos 288
A new pseudothelphusid crab from a cave in southern Costa Rica (Decapoda: Brachyura)
H. H. Hobbs III 295
Chirostylid and galatheid crustacean associates of coelenterates and echinoderms collected from the *Johnson-Sea-Link* submersible, including a new species of *Gastroptychus*
A. L. Rice and J. E. Miller 299
Procambarus (*Girardiella*) *steigmani,* a new crayfish (Decapoda: Cambaridae) from a longgrass prairie in northeastern Texas
Horton H. Hobbs, Jr. 309
A new species of *Processa* from Bermuda (Crustacea: Decapoda: Caridea)
Raymond B. Manning and C. W. Hart, Jr. 317
A new genus and species of neotropical water beetle, *Jolyelmis auyana,* from a Venezuelan Tepui (Coleoptera: Elmidae)
Paul J. Spangler and Robin A. Faitoute 322
Parmops coruscans, a new genus and species of flashlight fish (Beryciformes: Anomalopidae) from the South Pacific
Richard H. Rosenblatt and G. David Johnson 328
A new species of the anthiine genus *Plectranthias* (Pisces: Serranidae) from the Sala y Gómez Ridge in the eastern South Pacific, with comments on *P. exsul*
William D. Anderson, Jr. and John E. Randall 335
Gymnothorax parini, a new species of moray eel (Teleostei: Muraenidae) from Walters Shoals, Madagascar Ridge
Bruce B. Collette, David G. Smith, and Eugenia B. Böhlke 344
Geographic distribution of *Micronycteris schmidtorum* Sanborn (Chiroptera: Phyllostomidae)
César F. Ascorra, Don E. Wilson, and Alfred L. Gardner 351
A new subspecies of the Double-crested Cormorant, *Phalacrocorax auritus,* from San Salvador, Bahama Islands
George E. Watson, Storrs L. Olson, and J. Robert Miller 356
Systematics of the coatis, genus *Nasua* (Mammalia: Procyonidae)
Denise M. Decker 370
A new species of *Chrotomys* (Rodentia: Muridae) from Luzon Island, Philippines
Eric A. Rickart and Lawrence R. Heaney 387
The mammals of Catanduanes Island: Implications for the biogeography of small land-bridge islands in the Philippines
Lawrence R. Heaney, Pedro C. Gonzales, Ruth C. B. Utzurrum, and Eric A. Rickart 399
International Commission on Zoological Nomenclature 416
Reviewers—1990 417

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

SMITHSONIAN
OCT 24 1991
LIBRARIES

VOLUME 104 NUMBER 3
25 SEPTEMBER 1991
ISSN 0006-324X

THE BIOLOGICAL SOCIETY OF WASHINGTON

1990–1991

Officers

President: Leslie W. Knapp
President-elect: Storrs L. Olson
Secretary: G. David Johnson
Treasurer: Michael Vecchione

Elected Council

Roger F. Cressey, Jr.
Janet R. Gomon
Robert Hershler
Janet W. Reid
Wayne C. Starnes
Jeffery T. Williams

Custodian of Publications: Austin B. Williams

PROCEEDINGS

Editor: C. Brian Robbins

Associate Editors

Classical Languages: George C. Steyskal
Plants: David B. Lellinger
Insects: Wayne N. Mathis
Invertebrates: Jon L. Norenburg
Frank D. Ferrari
Rafael Lemaitre
Vertebrates: G. David Johnson

Membership in the Society is open to anyone who wishes to join. There are no prerequisites. Annual dues of $15.00 ($20.00 to non-USA addresses) include subscription to the *Proceedings of the Biological Society of Washington.* Library subscriptions to the *Proceedings* are: $25.00 within the U.S.A., $30.00 elsewhere.

The *Proceedings of the Biological Society of Washington* (USPS 404-750) is issued quarterly. Back issues of the *Proceedings* and the *Bulletin of the Biological Society of Washington* (issued sporadically) are available. Correspondence dealing with membership and subscriptions should be sent to The Treasurer, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Manuscripts, corrected proofs, editorial questions should be sent to the Editor, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Known office of publication: National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Printed for the Society by Allen Press, Inc., Lawrence, Kansas 66044

Second class postage paid at Washington, D.C., and additional mailing office.

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, National Museum of Natural History, Washington, D.C. 20560.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 419–435

MORPHOMETRIC DIFFERENTIATION AMONG WEST AFRICAN POPULATIONS OF THE RODENT GENUS *DASYMYS* (MUROIDEA: MURINAE), AND ITS TAXONOMIC IMPLICATIONS

Michael D. Carleton and Christine Martinez

Abstract.—Craniodental variation among West African samples of *Dasymys* is reassessed based on the larger museum series now available. Two morphological kinds can be discerned in this region and are referable to the locally available epithets *Dasymys rufulus* Miller (1900), described from Mount Coffee, Liberia, and *Dasymys foxi* Thomas (1912), named from Panyam, Nigeria. The degree of craniodental differentiation between these two phena matches that documented for other congeneric pairs of murid rodent species inhabiting parts of West Africa. *Dasymys rufulus* differs from *D. foxi* by its overall smaller size, especially as observed in its smaller, narrower cranium and less robust molars. In West Africa, samples of *D. rufulus* are broadly distributed from east of the Niger River, Nigeria, west to northern Sierra Leone; whereas, the known examples of *D. foxi* are restricted to the Jos Plateau in Nigeria. *Dasymys rufulus* and *D. foxi* are provisionally accorded specific status until taxonomic studies of *Dasymys* populations from other parts of Africa are undertaken to determine their relationships and distributional limits. It is doubtful that either form, but especially *D. rufulus,* is synonymous with *D. nudipes* or *D. incomtus.*

Shaggy-furred or marsh rats of the genus *Dasymys* are broadly if intermittently distributed over much of Africa south of the Sahara Desert, inhabiting a variety of wetland areas with thick ground cover. Current classifications recognize a single species, *Dasymys incomtus* (Sundevall, 1847), throughout this broad range (Misonne 1974, Honacki et al. 1982, Corbet & Hill 1986). The genus has not always been viewed as monotypic, for 13 of the 20 species-group taxa associated with *Dasymys* have been named as species. As of 1939, Allen listed 10 species, four of them containing from two to four subspecies.

The current perception of species diversity in *Dasymys* originated with Ellerman's (1941) treatment of the genus. Ellerman (1941:121) regarded all named forms, except *orthos* Heller (1911) which he did not examine, as races of *D. incomtus*: "It appears very unlikely that there is more than one species of this genus." His conviction in this regard may have been influenced by Osgood's (1936:256) earlier observation that "Both external and cranial characters in this genus are elusive and the range of variation throughout is comparatively slight," which he offered in the description of *D. incomtus griseifrons.* Except for the occasional retention of *D. nudipes* as a species (Roberts 1951, Crawford-Cabral 1983), subsequent classifications and regional catalogues have uniformly acknowledged the one species *D. incomtus* (for example, Ellerman et al. 1953, Hanney 1965, Rosevear 1969, Delany 1975, De Graff 1981, Meester et al. 1986, Happold 1987). A notable omission in arriving at the current species arrangement of shaggy-furred rats has been the presentation of data supportive of these taxonomic changes. The basis for recognition of a single species

has hinged on Ellerman's surmise that "it appears very unlikely" that more than one exists.

The present study contributes distributional and morphological information that bears on the status of *Dasymys* populations inhabiting portions of West Africa, namely from Nigeria west to Sierra Leone. Compared to the number of forms described from eastern and southern Africa, the taxonomy of shaggy-furred rats is less problematic in West Africa, where only two forms have been described: *Dasymys rufulus* Miller (1900) from Mount Coffee, Liberia, and *Dasymys foxi* Thomas (1912) from Panyam, on the Jos Plateau, Nigeria. Clarification of patterns of morphological variation on a regional basis, set within the context of local taxonomic designations, marks a necessary step toward refining the species taxonomy of *Dasymys* as a whole and gaining insight into its historical zoogeography.

Like other forms of *Dasymys,* Miller's *rufulus* and Thomas' *foxi* were viewed as subspecies of *D. incomtus* by Ellerman (1941), an arrangement which has persisted to the present day (Rosevear 1969, Misonne 1974, Happold 1987). Rosevear (1969:311) even questioned the validity of maintaining any formal racial division among West African populations: ". . . the differences in size between this race [that is, *rufulus*] and *foxi* are really very slight and it is open to some doubt whether the distinction can be retained." Happold (1987:132) formed a similar impression based on his review of Nigerian samples, noting that, in general, the smaller *rufulus* occurs in southern localities and the larger *foxi* in northern ones, but that ". . . the subspecific distinction may not be valid." These assessments deserve review based upon the larger museum series of West African *Dasymys* now available.

Materials and Methods

Approximately 300 specimens, consisting of conventional study skins with associated skulls, were examined (see Taxonomic Summary) from the following collections, their acronyms listed in parentheses: American Museum of Natural History, New York City (AMNH); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); and the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Preparation of the distribution map was based on locality information and geographical coordinates basically as given by collectors on specimen tags. We also consulted the gazetteers provided by Davis & Misonne (1964), Rosevear (1965) and Happold (1987), to verify the plotting of these sites and to obtain geographical coordinates not listed by collectors.

Several dimensions of the skin and skull were recorded in millimeters (mm) to characterize the morphology of the samples. Total length, tail length (TL), and hindfoot length (HFL) were extracted to the nearest whole mm from the skin tag, as was field weight to the nearest whole gram (gm). Length of the head and body (HBL) was obtained by subtracting the tail from total length. Fourteen cranial and two dental measurements were taken to the nearest 0.01 mm by means of hand-held digital calipers accurate to 0.02 mm. These measurements, and their abbreviations as used herein, include: occipitonasal length (ONL); greatest zygomatic breadth (ZB); breadth of the braincase (BBC); least interorbital breadth (IOB); length of the rostrum (LR); breadth of the rostrum (BR); postpalatal length (PPL); length of the bony palate (LBP); length of the incisive foramen (LIF); length of the diastema (LD); breadth of the bony palate across the upper first molars (BM1s); breadth of the zygomatic plate (BZP); length of the auditory bullae (LAB); breadth across the exoccipital condyles (BEC); crown length of the maxillary toothrow (LM1–3); and width of the upper first molar (WM1). The limits of most of these dimensions on the murine skull are defined and illustrated by Musser (1979).

Recording of measurements was limited to animals judged to be adult based on the possession of fully erupted third molars and adult pelage. "Adult" animals were further segregated into crude age classes based on upper molar wear as follows.

Young adult.—Tricusp arrangement of first and second chevrons of M1–2 well defined, the enamel borders of the medial (t1 and t3) and lateral (t3 and t6) cusps deeply constricted and contiguous or virtually so; dentinal lakes of chevrons thus narrow and discontinuous transversely or nearly so; M3 erupted and slightly worn; t1s on M2–3 wholly isolated from enamel borders of second chevron; transverse enamel valleys between chevrons deep and extend across the width of the molar.

Full adult.—Enamel indentations of the medial and lateral cusps on chevrons of M1–2 not in contact, their dentin basins broader and continuous across the width of the tooth; enamel, less often the dentin, of t1s on M2–3 connected to that of the second chevron (anterior border of t5).

Old adult.—Occlusal wear heavy such that the dentin of chevrons, particularly the middle one and t8, cross-connected at their medial and lateral edges; enamel valleys separating chevrons appear as islands surrounded by dentinal basins.

Although the above data were recorded for all specimens examined, the multivariate analyses were applied to the larger population samples with the highest incidence of intact crania. These are:

OTU G3.—Ghana, Pulima, $n = 37$.

OTU I1.—Ivory Coast, Kong, $n = 10$.

OTU I2.—Ivory Coast, Sienso, $n = 15$.

OTU L1.—Liberia, Mount Coffee, $n = 5$ (type series of *rufulus*).

OTU N4.—Nigeria, Dada, $n = 24$.

OTU N10.—Nigeria, Jos Plateau, Panyam Fish Farm, $n = 43$ (near type locality of *foxi*).

OTU T3.—Togo, Padori, $n = 11$.

Standard descriptive statistics (mean, range, standard deviation) were derived for the OTUs (see Appendix 1). One-way analyses of variances were applied to the three largest OTUs (G3, N4, and N10) to assess the effect of gender on the variation of the 16 craniodental variables. Principal components were extracted from a variance-covariance matrix and computed using the craniodental variables after transformation to their natural logarithms. Loadings are expressed as Pearson product-moment correlation coefficients of the principal components with the original cranial variables. All analytic procedures were carried out using Systat (Version 4.1, 1989), a series of statistical routines programmed for microcomputers.

Morphometric Results

Sexual dimorphism in cranial size is unappreciable within populations of *Dasymys,* a finding in agreement with biometric studies of other African murines (for example, Van der Straeten & Verheyen 1981, 1982; Carleton & Robbins 1985). Among the three largest population samples analyzed, only six cranial dimensions vary significantly with regard to gender (Table 1), with males larger in each instance, and each significant variable is unique to a particular sample. We attribute the sporadic occurrence of significant findings across the three samples to a combination of Type I sampling errors and unequal age representation among the sexes of each sample. For example, within the Panyam sample (N10), males are disproportionately represented in the adult (12 to 9) and old adult (2 to 0) age groups. As discussed below, age can contribute substantial intrapopulation variation. In view of the negligible or inconsistent effects, particularly with regard to the magnitude of interlocality differentiation, both sexes were included in the multivariate analyses.

With the large series available from near the type locality of *D. foxi,* populations in Nigeria have provided critical insight to the morphological differentiation among West African *Dasymys.* Thomas (1912) diagnosed *D. foxi* on the basis of its larger

Table 1.—*f* values from one-way anovas (effect = sex) of three population samples of West African *Dasymys*.

Cranial variables	Ghana: Pulima (14 ♂, 23 ♀)	Nigeria: Dada (8 ♂, 15 ♀)	Nigeria: Panyam (22 ♂, 16 ♀)
ONL	0.31	1.27	3.96
ZB	0.01	2.11	2.65
BBC	0.43	6.17*	1.54
IOB	5.70*	0.11	0.63
LR	0.52	0.06	3.70
BR	0.48	0.29	5.46*
PPL	0.54	0.49	2.47
LBP	0.10	0.62	6.83*
LIF	0.61	0.01	0.83
LD	0.70	0.63	3.17
LM1–3	1.69	2.06	0.01
WM1	0.13	0.84	0.06
BM1s	0.01	0.51	0.02
BZP	0.11	1.41	0.16
LAB	0.22	13.68**	0.42
BEC	0.61	2.83	11.62**

* = $P \leq 0.05$; ** = $P \leq 0.01$.

size, especially as observed in the length and breadth of the molar rows. Such differences were borne out in principal component analyses of the two largest Nigerian samples, Dada and Panyam Fish Farm, whose scores overlapped little in multivariate space (Fig. 1). The uniformly positive and high correlations of most craniodental variables with the first principal component suggest a general size factor (Table 2) and emphasize the overall larger size of the Panyam specimens. The dispersion of individuals along the second principal component reflects certain breadth measurements (BEC, IOB) and size of the molars (LM1–3, WM1), which again reflect the broader cranium and more robust molars recorded for the specimens from the vicinity of Panyam.

Some age-related size variation undoubtedly contributes to the elliptical spread observed for each population sample in the bivariate plot of the first two principal com-

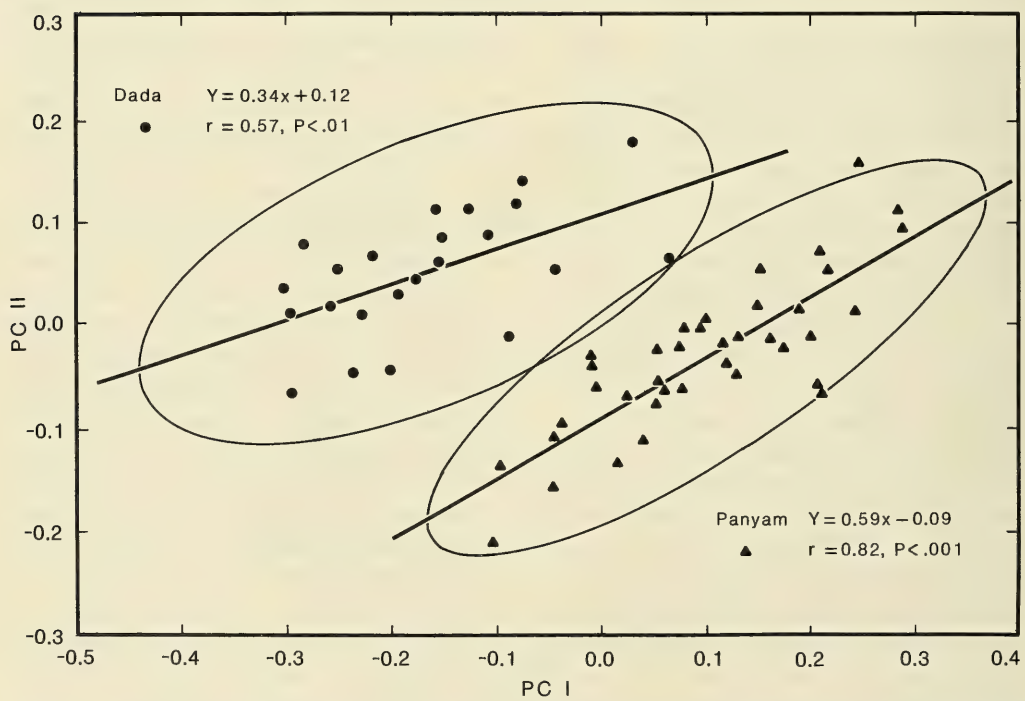


Fig. 1. Projection of individual specimen scores on the first two principal components for the two largest samples of Nigerian *Dasymys*, Dada (n = 23) and vicinity of Panyam (n = 38). Ellipses correspond to 95% confidence envelopes for scores of individuals within each sample. See Table 2.

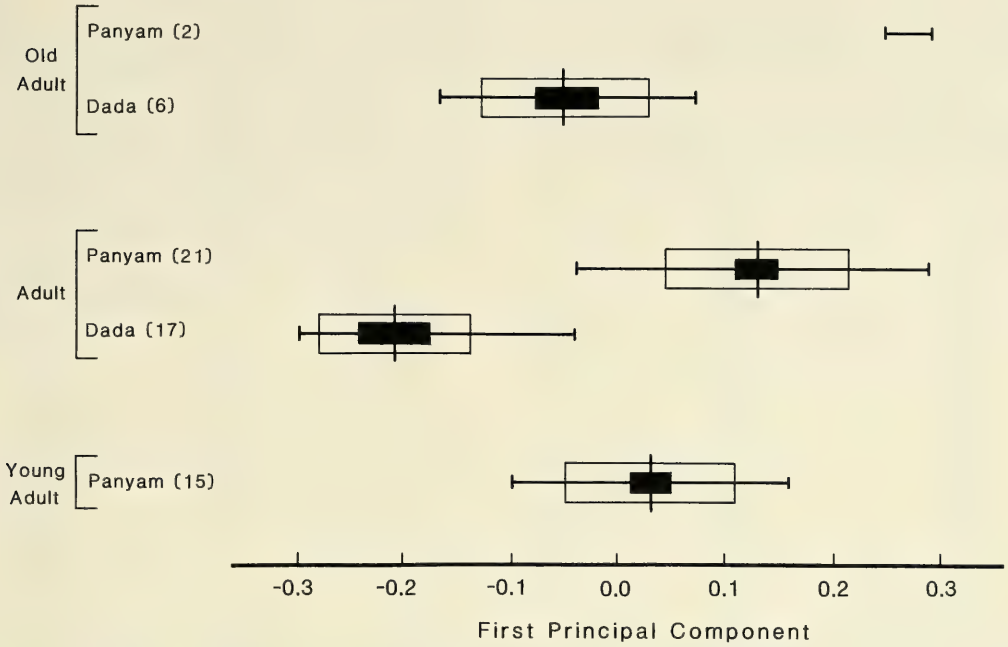


Fig. 2. Box plots of first principal component scores (see Fig. 1) of Dada and Panyam samples arranged by three adult age classes. Mean (vertical line), one standard error of the mean (closed rectangle), one standard deviation (open rectangle), and the range (horizonal line) are indicated.

ponents (Fig. 1). The range of factor scores viewed by age class suggests such an influence, especially for the first principal component (Fig. 2). Still, a marked separation between the Dada and Panyam samples is apparent for a given age class. The absence of specimens classified as young adults in the Dada sample probably accounts for its wider confidence ellipse as well as the marginally significant difference ($P = 0.052$) in the slopes of their regression equations.

Rotation (varimax procedure) of the principal components underscored the same disparity in cranial breadth (ZB, BBC, IOB, BEC) and molar size (LM1–3, WM1) between the Dada and Panyam samples, as well as in the LAB (Table 2). One-way analyses of variance, using locality as the category of effect, generally corroborated the higher variability of these dimensions, with WM1, BEC, and LM1–3 exhibiting the largest f values, respectively (Table 2). Although the principal component and anova results are here reported only for the Dada and Panyam samples, all Nigerian specimens with intact skulls were subjected to the same analyses and revealed the same pattern of dual clouds of points. Specimens from the Jos Plateau (Panyam Fish Farm, 2 mi N Panyam, and Ugar Jabar), which represent Thomas' (1912) *D. foxi,* formed one of those constellations, whereas the other corresponded to specimens from all other localities in Nigeria (see Specimens Examined).

The distinctiveness of the animals from the vicinity of Panyam is still apparent in principal component analyses including samples from four other West African countries (Fig. 3). Again, overall larger size—in particular as expressed by the IOB, BEC, LAB, LM1–3, and WM1—contributed to the separation of this Nigerian sample from other West African *Dasymys* (Table 3). Confidence ellipses for the centroids of the latter populations, including the Dada sam-

Table 2.—Results of principal component analyses and one-way anovas (effect = locality) for Dada (n = 23) and Panyam (n = 38) samples of *Dasymys* (see text and Fig. 2).

Cranial variables	Unrotated		Rotated		f (locality)[1]
	PC I	PC II	PC I	PC II	
ONL	0.92	0.29	0.88	0.34	37.0
ZB	0.90	0.04	0.68	0.52	54.8
BBC	0.79	−0.21	0.45	0.65	59.8
IOB	0.52	−0.53	0.02	0.73	37.5
LR	0.79	0.44	0.84	0.14	15.8
BR	0.74	0.29	0.81	0.24	9.9
PPL	0.88	0.29	0.86	0.32	29.3
LBP	0.59	0.11	0.40	0.27	12.2
LIF	0.71	0.29	0.76	0.22	14.9
LD	0.81	0.47	0.89	0.13	12.6
LM1–3	0.76	−0.46	0.25	0.83	119.7
WM1	0.75	−0.61	0.15	0.94	273.7
BM1s	0.84	0.04	0.51	0.47	27.7
BZP	0.77	0.25	0.41	0.24	20.2
LAB	0.79	−0.27	0.47	0.71	76.0
BEC	0.77	−0.43	0.35	0.82	194.5
Eigenvalue	0.027	0.006	0.016	0.014	
% Variance	60.4	14.0	34.1	31.2	

[1] All f values significant at $P \leq 0.01$.

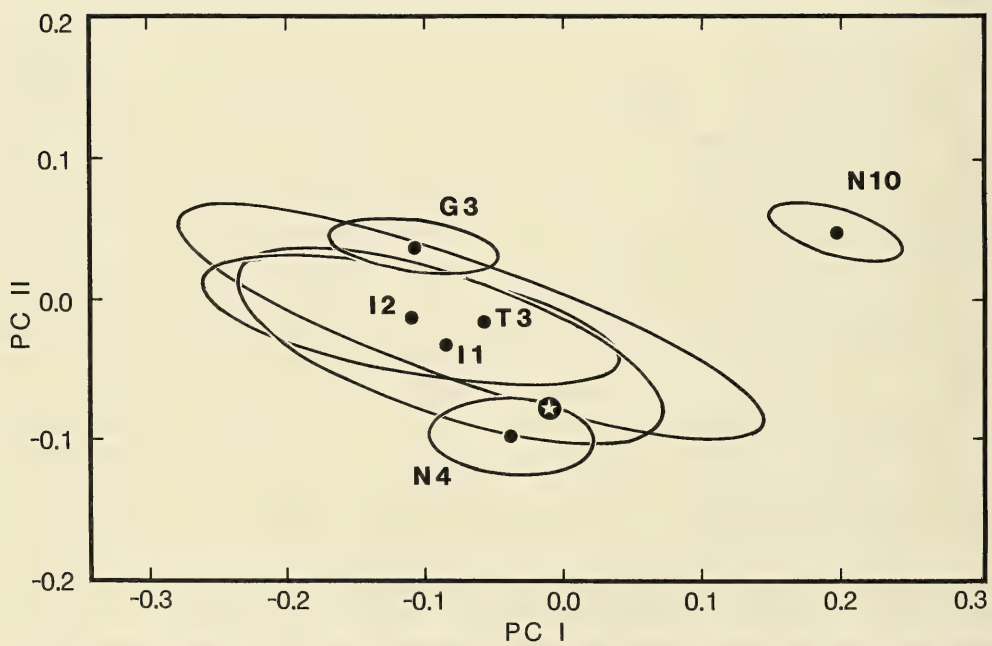


Fig. 3. Projection of group centroids on the first two principal components for six largest samples of West African *Dasymys* (see Table 3; sample codes and sizes are given in Materials and Methods). Ellipses correspond to 95% confidence limits of a group's centroid. Enclosed star represents the holotype of *Dasymys rufulus* Miller (1900).

ple, were broadly congruent and circumscribed the data point that represents the type specimen (USNM 83844) of Miller's (1900) *D. rufulus*. Although we did not personally examine the type material of *D. foxi*, the cranial measurements of the holotype (BMNH 12.4.3.15 from Panyam) supplied by Dr. Erik Van der Straeten clearly depict a robust skull that fits with the USNM series from the Jos Plateau.

Discussion

Several of the common names applied to *Dasymys*—namely, "marsh," "swamp," or "water" rats—underscore the regular association of these rodents with various kinds of wetland environments. Typical habitat references include stream and river banks, marshy areas with reed beds, swampy edges along rivers, lush grass covering moist ground, matted semi-aquatic grasses and sedges, wetter parts of floodplains, and highland bogs (Rosevear 1969, Smithers 1971, Sheppe 1972, Kingdon 1974). In addition to preferring generally wet conditions, the presence of dense ground cover appears critical to their ecological occurrence in affording protected runways and nesting sites. Their diet is thought to consist principally of green vegetable matter, yet some insects remains have been identified in stomach contents (Hanney 1965, Smithers 1971, Coe 1975). Shaggy-furred rats appear to be mostly terrestrial, although semi-aquatic habits have been noted, and their activity has been described as principally nocturnal but to a limited extent diurnal (Thomas 1912, Roberts 1951, Smithers 1971, De Graaff 1981).

Knowledge of the life history and ecology of *Dasymys*, however, remains sketchy and stems largely from trapping experiences related in faunal accounts and from collectors' notations on specimen tags. Thorough field studies on the biology of this genus have yet to be conducted, a situation which leaves unanswered whether some of the apparent variation in habitat and habit reflects populational or specific differences.

Table 3.—Results of principal component analysis using six largest OTUs of *Dasymys* (n = 130) (see text and Fig. 3).

Cranial variables	PC I	PC II	PC III
ONL	0.96	−0.18	0.09
ZB	0.89	0.03	0.05
BBC	0.76	0.19	0.16
IOB	0.30	0.58	0.16
LR	0.87	−0.33	0.08
BR	0.81	−0.24	0.13
PPL	0.92	−0.09	0.05
LBP	0.68	−0.14	−0.17
LIF	0.80	−0.15	0.22
LD	0.91	−0.27	0.07
LM1–3	0.61	0.60	0.17
WM1	0.51	0.74	0.16
BM1s	0.87	0.05	−0.01
BZP	0.78	0.16	−0.59
LAB	0.71	0.41	0.12
BEC	0.68	0.37	0.16
Eigenvalue	0.033	0.005	0.003
% Variance	63.5	10.4	5.9

In West Africa, the pattern of morphological variation supports the existence of two separate species, to which the closest regional epithets *Dasymys rufulus* Miller (1900) and *Dasymys foxi* Thomas (1912) apply. The marked discrimination between these two sets of populations clearly disputes the notions that the traits of *rufulus* and *foxi* are insufficiently marked for even subspecific recognition or that they intergrade imperceptibly in size along a north-south cline (Rosevear 1969, Happold 1987). Instead, the craniodental differentiation observed between populations of each resembles that demonstrated for other pairs of congeneric species inhabiting portions of West Africa—for example those of *Hybomys, Lemniscomys, Malacomys,* and *Praomys* (Van der Straeten & Verheyen 1978, 1979, 1981, 1982; Carleton & Robbins 1985).

How these two species in West Africa relate to forms of *Dasymys* described from central, eastern, and southern Africa will

Fig. 4. Views of the cranium and mandible of an adult male *Dasymys foxi* (USNM 403644) from the vicinity of Panyam, Nigeria. Approximately ×1.75.

require careful revisionary attention to the entire genus, which is beyond the scope of our paper. The primary descriptive literature on *Dasymys* lends few clues.

Miller (1900) contrasted his new species *Dasymys rufulus* to *D. bentleyae* and *D. incomtus,* but had at hand for examination only a single specimen of the latter (probably USNM 101884 from Port Natal, South Africa). His enumeration of the differences between *D. rufulus* and *D. incomtus* is apt and emphasized the generally smaller size and more rufous pelage of the former relative to the larger skull, robust molars, and dark-toned pelage of the latter. These morphological contrasts are apparent in more recently collected examples of *D. incomtus* available to us from South Africa and Zim-

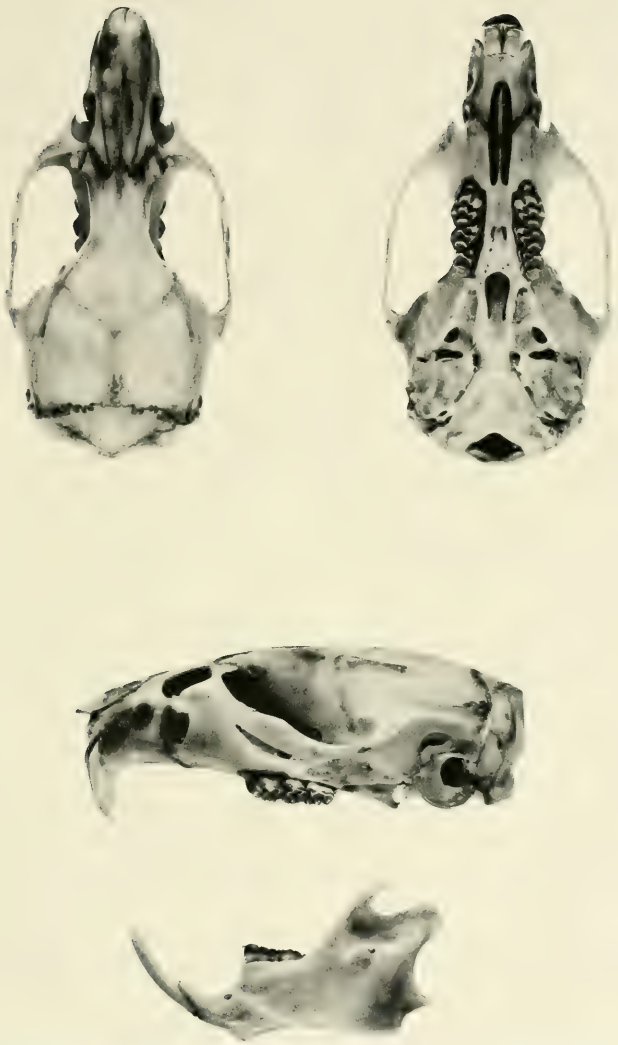


Fig. 5. Views of the cranium and mandible of an adult male *Dasymys rufulus* (USNM 83901) from Mount Coffee, Liberia. Approximately ×1.75.

babwe. The eastern distributional limits of *rufulus* are uncertain; examples that we have seen from Cameroon (AMNH specimens from Tongo and Ndokayo) are referable to *rufulus*.

In his description of *Dasymys foxi,* Thomas (1912) had available for examination examples of *D. rufulus,* as well as specimens of *Dasymys* from other regions of Africa contained in the British Museum (Natural History). With only passing mention, he dismissed Miller's (1900) *D. rufulus* as a close relative of *D. foxi,* based principally on the former's smaller molar rows, and instead focussed his comparisons to *D. medius* from central Africa.

Our principal component analyses corroborate Thomas' (1912) emphasis of molar size as a cardinal trait for distinguishing *D. foxi* from *D. rufulus.* The distinction rests not only with the greater length of the toothrows in *D. foxi* but also with their greater width (Tables 2, 3; Appendix 1). Breadth measurements across the zygoma and

braincase contribute substantially to the robust appearance of the skull of *D. foxi* versus that of *D. rufulus* (Figs. 4, 5), in general relatively more so than length variables (Table 2), although specimens of *D. foxi* do average larger in most cranial dimensions (Appendix 1). Field weights and external measurements of the skin similarly reflect the larger size of *D. foxi,* but overlap in ranges is appreciable (Appendix 1). Examples of *D. foxi* and *D. rufulus* are practically inseparable on the basis of pelage coloration: both exhibit a grayish to reddish brown dorsum and a light to dark gray venter with varying concentrations of a creamy-buff wash. Red tones seem more predominant in the dorsum of *D. rufulus* and gray in *D. foxi,* but this impression is undermined by the range of chromatic variation observed within series of each form.

We have not yet examined series of *D. medius* to form an opinion on its degree of similarity of *D. foxi.* In external and cranial size, however, specimens of *D. foxi* closely resemble those of *D. incomtus,* as known to us from several localities in South Africa and Zimbabwe. The agreement is particularly strong in their possession of heavily constructed, long toothrows. Like *D. rufulus* the pelage color of *D. foxi* contrasts with the darker, grayish-black upper parts typical of *D. incomtus.* Moreover, the texture of its fur seems finer relative to both *D. foxi* and *D. rufulus.* The taxonomic significance of these pelage differences must await rigorous evaluation of variation using large series of *D. incomtus* and determination of its relationship with forms described from eastern and central Africa.

Miller (1900) erred in reporting five plantar pads as characteristic of *D. rufulus.* A sixth pad, the hypothenar, is present and, although small, is clearly discernable on the dried hind feet of most specimens comprising his type series. A total of six plantar pads also appears characterisitic of *D. foxi* and of most other *Dasymys* from central, eastern, and southern Africa, which represent a variety of taxa including *incomtus* proper. Only examples of *D. nudipes* seem to typically lack a sixth pad (Hill & Carter 1941, Crawford-Cabral 1983), but we have examined too few specimens of this taxon to judge the constancy of the trait. In other features as well—more brightly colored dorsal and ventral pelage, large size (hind foot length typically 38 to 42 mm), and the usual presence of a tiny t3 on the upper second molar—*nudipes* represents a well-marked form that probably warrants specific status (also see Crawford-Cabral 1983 and Crawford-Cabral & Pacheco 1989).

Available data on chromosomal variation in the genus *Dasymys* is limited to standard karyotypic preparations. Matthey (1958) reported a diploid number of 38, with four pairs of biarmed autosomes, for a sample (number of individuals unknown) of *Dasymys* from Ivory Coast. Later, Tranier & Gautun (1979) obtained a similar figure for Ivory Coast *Dasymys,* 2N = 36 with six pairs of metacentrics and submetacentrics based on two males. Both records are presumably referable to *D. rufulus,* but the variation implied by these studies should be reconfirmed using larger samples of fresh material. The one karyotypic example from eastern Africa, a single male from Burundi, exhibited a 2N = 40, with six pairs of biarmed autosomes (Maddalena et al. 1989). The authors provisionally identified their specimen as *D. incomtus* but stressed the lack of chromosomal data based on true *incomtus* from South Africa. Although these studies suggest the potential value of karyotypic information in *Dasymys* systematics, the evidence is, as yet, too fragmentary to offer insight on species boundaries.

Unlike some other rodent species, samples of *Dasymys* from West Africa are not restricted to a particular faunal region or biome. Instead their geographic distribution spans several major biotic realms, including (per Delany & Happold 1979) lowland rain forest, Guinea savanna, and Sudan savanna (Fig. 6). Moist living conditions

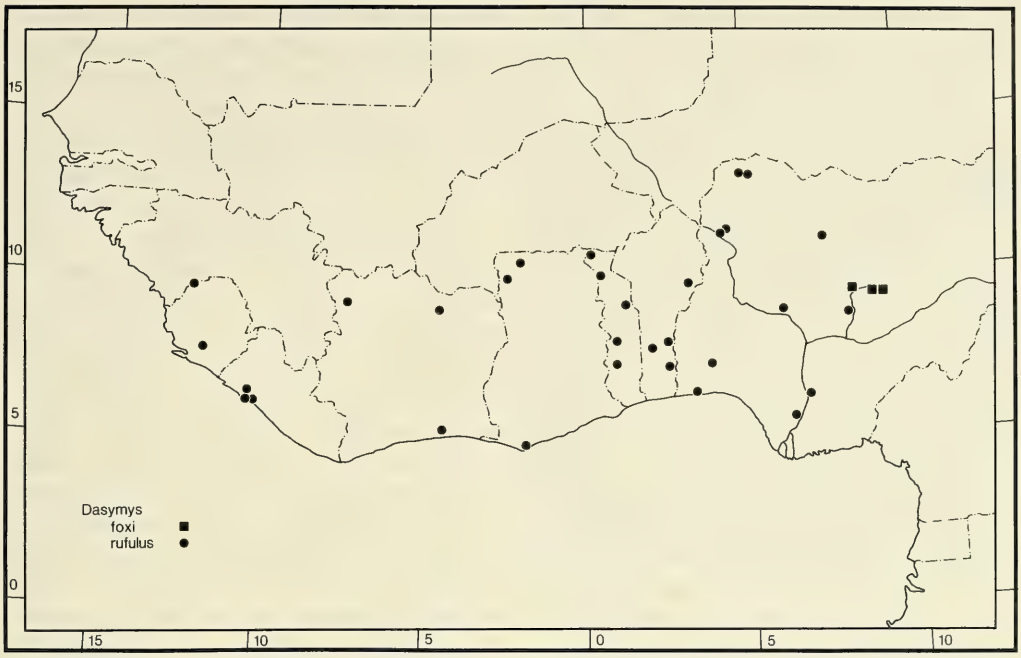


Fig. 6. Distribution map of West African *Dasymys* illustrating collecting localities reported herein (see Taxonomic Summary).

combined with dense ground cover, such as afforded by palustrine and riverine microhabitats within these vegetational zones, appear to be the critical factors that correspond to the presence of *Dasymys,* more so than the prevailing climatic, edaphic, and floristic features that typify these biomes. The inherently patchy nature of such wetland environments may account for the interrupted distribution among *Dasymys* populations. Moreover, the potential for geographic isolation and genetic differentiation within this ecological setting stands at odds with the notion of a single, pandemic species of shaggy-furred rat occurring throughout much of subSaharan Africa as portrayed in current classifications (Misonne 1974, Honacki et al. 1982, Corbet & Hill 1986).

The West African distribution of the two kinds of *Dasymys* identified herein, however, does correspond to one prominent ecogeographic feature. The few localities known for *D. foxi* are limited to the Jos Plateau, a highland mass in eastcentral Nigeria; whereas, populations of *D. rufulus* are widely documented across the entire region, from just east of the Niger River, Nigeria, west to northern Sierra Leone (Fig. 6). Isolated within northern Guinea savanna, the central plateau itself rises to 1000 meters, with isolated peaks reaching 1500 to 2000 m, and supports a predominantly grassland vegetation with extensive rocky outcrops and few trees. The Jos Plateau experiences a wetter and cooler climate compared to that of the surrounding Guinea savanna and harbors relictual stands of rain forest along its southern slope (Happold 1985). We have not detected any instance of sympatry, but the two forms occur in close proximity in the vicinity of the Mada River, along the western edge of the plateau. Distributional transects in this region, as well as the southern slopes, would be highly informative.

Within Nigeria, Happold (1985, 1987) listed six species of mammals as restricted to this highland area—three rodents (*Ta-*

terillus nigeriae, Dendromus melanotis, and *Cryptomys ochraceocinereus*), two bats (*Rhinolophus alticolus* and *Miniopterus inflatus*), and one artiodactyl (*Oreotragus oreotragus*). In view of this modest level of endemism and its distinctive bioclimatic features, Happold recognized the Jos Plateau as one of eight major faunal regions within the country. He further suggested that the Plateau and the Cameroon highlands, located 500 km to the east, share certain faunal similarites (without elaborating these in detail). *Dasymys foxi* may qualify as another mammalian species whose distribution in West Africa is localized to the Jos Plateau and whose nearest relatives occur far outside the region to the east. Such a viewpoint accords with Thomas' (1912) original comparisons of *foxi* and *medius,* a form described from Mount Ruwenzori in the Rift Valley system. Nevertheless, as cautioned by Happold (1985), the establishment of past biotic links between the Jos Plateau and other regions of Africa must await better documentation of the Plateau's mammalian fauna. Of equal importance are the basic needs for alpha-level revisionary studies of the mammals occurring there and for persuasive arguments of interspecific relationships.

In summary, populations of *Dasymys* inhabiting other parts of Africa also exhibit substantial morphological variation, much of it grossly apparent as large-bodied animals with robust skulls and molars versus those with smaller proportions. Thus, whether *rufulus* or *foxi,* or perhaps both names, will prove to be junior synonyms of species described from other regions is uncertain at this stage of our taxonomic understanding of the genus. Although inspection of additional museum material indicates the occurrence of large and small forms in other geographic areas, we doubt that only two species, separated principally on size, exist over the vast subSaharan region. As noted above, *D. nudipes* is appreciably differentiated from both *rufulus* and *foxi,* as well as from *D. incomtus.* The greater taxonomic complexity of the genus is further suggested by the preliminary study of Crawford-Cabral and Pacheco (1989), who detected four distinctive forms (*nudipes, incomtus, bentleyae,* and *fuscus*) in southern Africa but formally recognized only *D. nudipes* as a separate species.

There is little evidence to indicate that *rufulus* will be found to intergrade with populations of *D. incomtus.* The possibility that *foxi* and *D. incomtus* are conspecific seems more plausible, but such a hypothesis needs to be carefully evaluated before accepting this nomenclatural action. Critical insight to the geographic limits and relationships of the two West African taxa will require taxonomic studies of other populations of *Dasymys,* particularly those in central and eastern Africa where some ten forms have been described, all of them now regarded as subspecies of *D. incomtus* (Ellerman 1941, Misonne 1974). Until such results are forthcoming, we here list the specimens examined under the appropriate specific designations available for populations within the West African region.

Taxonomic Summary

Dasymys rufulus Miller

Dasymys rufulus Miller, 1900:639 (type locality, Liberia, Mount Coffee; holotype, USNM 83844).—Allen, 1939:383.

Dasymys incomtus rufulus, Ellerman, 1941: 123.—Rosevear, 1965:311.—Misonne, 1974:19.—Happold, 1987:132.

Specimens examined.—DAHOMEY: Diho, Central Region, 08°05′N, 02°31′E, 1 (USNM); Kétou, Eastern Region, 07°21′N, 02°37′E, 2 (USNM); Nikki, Borgou Region, 09°56′N, 03°13′E, 3 (USNM); Zizonkamé, Central Region, 07°55′N, 02°01′E, 2 (USNM). GHANA: Efeipo Krom, Western Region, 04°57′N, 01°52′W, 1 (USNM); Pirisi, Upper Region, 10°07′N, 02°27′W, 5 (USNM); Pulima, Upper Region, 10°51′N,

02°03′W, 50 (USNM). IVORY COAST: 20 km NW Dabou, 05°25′N, 04°33′W, 2 (AMNH); Kong, Upper Region, 09°09′N, 04°37′W, 10 (USNM); Sienso, 09°25′N, 07°31′W, 26 (USNM). LIBERIA: Du River, Firestone Camp No. 3, 1 (MCZ); Du River, Harbel, 1 (MCZ); Duside, 37 (AMNH); Mount Coffee, 06°30′N, 10°35′W, 6 (USNM, holotype and type series). NIGERIA: Agoleri, 1.5 mi E, 06°22′N, 06°52′E, 1 (USNM); Ashaka, 05°38′N, 06°24′E, 1 (USNM); Dada, Northern Region, 11°34′N, 04°29′E, 37 (USNM); Ibadan, University of Ife, 07°23′N, 03°54′E, 6 (USNM); Iella, 2 mi E Bahindi, Northern Region, 2 (USNM); Mada River, 3 mi E Gudi, Northern Region, 08°54′N, 08°17′E, 2 (USNM); Sokoto, 12 mi N, 1 (USNM); Tangaza, Northern Region, 1 (USNM); Tsanchaga, 8 mi E Bida, Northern Region, 2 (USNM); University of Lagos, Federal District, 7 (USNM); Zaria, 15 mi NW, 1 (USNM). SIERRA LEONE: Sainya, 5.2 mi (by road) W Outamba-Kilimi National Park, Northern Province, 09°48′N, 12°27′W, 1 (USNM); Yengema, 07°49′N, 12°27′W, 2 (USNM). TOGO: Dapongo, 10°52′N, 00°13′E, 1 (USNM); Ezimé, 07°29′N, 00°56′E, 1 (USNM); Padori, 10°13′N, 00°25′E, 11 (USNM); Pagola, 08°11′N, 00°58′E, 4 (USNM); Pewa, 09°17′N, 01°14′E, 1 (USNM). TOTAL = 227.

Dasymys foxi Thomas

Dasymys foxi Thomas, 1912:685 (type locality, Nigeria, Panyam, 4000 ft; holotype, BMNH 12.4.3.15).—Allen, 1939: 382.

Dasymys incomtus foxi, Ellerman, 1941: 122.—Rosevear, 1965:312.—Misonne, 1974:19.—Happold, 1987:132.

Specimens examined.—NIGERIA: 2 mi N Panyam, 09°27′N, 09°09′E, 3 (USNM); Panyam Fish Farm, Jos Plateau, 09°27′N, 09°12′E, 52 (USNM); Ugar Jabar, 2 mi N Jemaa, Jos Plateau, Northern Region, 09°31′N, 08°23′E, 4 (USNM). TOTAL = 59.

Acknowledgments

We thank Guy G. Musser (AMNH) and Maria Rutzmoser (MCZ) for allowing us to examine specimens under their care. Dave Schmidt carefully prepared the various figures, undertook the cranial photography, and assisted with the verification of locality data. We appreciate the careful attention that he brings to these essential tasks. The manuscript was reviewed by Drs. Guy G. Musser (AMNH) and Erik Van der Straeten (Universiteit Antwerpen). Dr. Van der Straeten kindly provided his own mensural data on the holotype of *Dasymys foxi* in the BMNH.

Literature Cited

Allen, G. M. 1939. A checklist of African mammals.—Bulletin of the Museum of Comparative Zoology, Harvard 83:1–763.

Carleton, M. D., & C. B. Robbins. 1985. On the status and affinities of *Hybomys planifrons* (Miller, 1900) (Rodentia: Muridae).—Proceedings of the Biological Society of Washington 98:956–1003.

Coe, M. 1975. Mammalian ecological studies on Mount Nimba, Liberia.—Mammalia 39:523–588.

Corbet, G. B., & J. E. Hill. 1986. A world list of mammalian species. Second edition. British Museum (Natural History), London, 254 pp.

Crawford-Cabral, J. 1983. Patterns of allopatric speciation in some Angolan Muridae.—Annales Musée Royal de L'Afrique Centrale, Sciences Zoologiques 237:153–157.

———, & A. Pacheco. 1989. A craniometrical study of some water rats of the genus *Dasymys* (Mammalia, Rodentia, Muridae).—Garcia de Orta, Series Zoologiques, Lisboa 15:11–24.

Davis, D. H. S., & X. Misonne. 1964. Gazetteer of collecting localities of African rodents.—Musée Royal de l'Afrique Centrale, Documentation Zoologique 7:1–100.

De Graaff, G. 1981. The rodents of southern Africa. Notes on their identification, distribution, ecology and taxonomy. Butterworths and Co., Durban, 267 pp.

Delany, M. J. 1975. The rodents of Uganda. British Museum (Natural History), London, 165 pp.

———, & D. C. D. Happold. 1979. Ecology of Af-

rican mammals. Longman Group Ltd., London, viii + 434.

Ellerman, J. R. 1941. The families and genera of living rodents. Volume II. Family Muridae. British Museum (Natural History), London, 690 pp.

———, T. C. S. Morrison-Scott, & R. W. Hayman. 1953. Southern African mammals 1758 to 1951: a reclassification. British Museum (Natural History), London, 363 pp.

Hanney, P. 1965. The Muridae of Malawi.—Journal of Zoology, London 146:577–633.

Happold, D. C. D. 1985. Geographical ecology of Nigerian mammals.—Annales Musée Royal de L'Afrique Centrale, Sciences Zoologiques 246: 5–49.

———. 1987. The mammals of Nigeria. Oxford University Press, New York, 402 pp.

Hill, J. E., & T. D. Carter. 1941. The mammals of Angola, Africa.—Bulletin of the American Museum of Natural History 78:1–211.

Honacki, J. H., K. E. Kinman, & J. W. Koeppl (eds.). 1982. Mammalian species of the world: a taxonomic and geographic reference. Allen Press, Inc. and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.

Kingdon, J. 1974. East African mammals. Volume IIB. Hares and rodents. University of Chicago Press, Chicago, 343–704.

Maddalena, T., E. Van der Straeten, L. Ntahuga, & A. Sparti. 1989. Nouvelles donnees et caryotypes des rongeurs du Burundi.—Revue Suisse Zoologie 96:939–948.

Matthey, R. 1958. Les chromosomes et la position systématique de quelques Murinae africains (Mammalia–Rodentia).—Acta Tropica 15:97–117.

Meester, J. A. J., I. L. Rautenbach, N. J. Dippenaar, & C. M. Baker. 1986. Classification of southern African mammals.—Transvaal Museum Mongraph 5:1–359.

Miller, G. S. 1900. A collection of small mammals from Mount Coffee, Liberia.—Proceedings of the Washington Academy of Sciences 2:631–649.

Misonne, X. 1974. Rodentia, main text. *In* J. Meester & H. W. Setzer, eds., The mammals of Africa, an identification manual, Part 6. Smithsonian Institution Press, Washington, D.C., 39 pp.

Musser, G. G. 1979. Results of the Archbold Expeditions. No. 102. The species of *Chiropodomys,* arboreal mice of Indochina and the Malay Archipelago.—Bulletin of the American Museum of Natural History 162:377–445.

Osgood, W. H. 1936. New and imperfectly known small mammals from Africa.—Zoological Series of the Field Museum of Natural History 20:217–256.

Rosevear, D. R. 1965. The bats of West Africa. British Museum (Natural History), London, 418 pp.

———. 1969. The rodents of West Africa. British Museum (Natural History), London, 604 pp.

Roberts, A. 1951. The mammals of South Africa. "The Mammals of South Africa" Book Fund, South Africa, 700 pp.

Sheppe, W. 1972. The annual cycle of small mammal populations on a Zambian floodplain.—Journal of Mammalogy 53:445–460.

Smithers, R. H. N. 1971. The mammals of Botswana.—National Museums of Rhodesia, Museum Memoir 4:1–340.

Thomas, O. 1912. List of a third collection of mammals from Panyam, N. Nigeria, presented by the Rev. G. T. Fox.—Annals and Magazine of Natural History, Series 8, 9:683–686.

Tranier, M., & J. C. Gautun. 1979. Recherches caryotypiques sur les rongeurs de Côte d'Ivoire: résultats préliminaires pour les milieux ouverts.—Mammalia 43:252–254.

Van der Straeten, E., & W. N. Verheyen. 1978. Karyological and morphological comparisons of *Lemniscomys striatus* (Linnaeus, 1758) and *Lemniscomys bellieri* Van der Straeten, 1975, from Ivory Coast (Mammalia: Muridae).—Bulletin of Carnegie Museum of Natural History 6: 41–47.

———, & ———. 1979. Notes taxonomiques sur les *Malacomys* de l'Ouest Africain avec redescription du patron chromosomique de *Malacomys edwardsi* (Mammalia, Muridae).—Revue de Zoologie Africaine 93:10–35.

———, & ———. 1981. Étude biometrique du genre *Praomys* en Côte d'Ivoire.—Bonner Zoologische Beiträge 32:249–264.

———, & ———. 1982. Differences biometrique entre *Hybomys univittatus* (Peters) et *Hybomys trivirgatus* (Temminck) de l'Afrique de l'ouest.—Bonner Zoologische Beiträge 33:205–213.

(MDC) Division of Mammals, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (CM) Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48104.

Appendix 1.—Cranial and external dimensions (in mm) of selected samples of *Dasymys*.

Species and OTU	*n*	Mean	Range	*SD*
		Occipitonasal Length		
D. rufulus				
Ghana (G3)	37	32.9	30.4–36.7	1.41
Ivory Coast (I2)	13	33.7	31.3–37.7	1.87
Liberia (L1)	5	34.8	32.9–35.8	1.13
Nigeria (N4)	24	34.2	32.5–36.2	1.08
D. foxi				
Nigeria (N10)	43	36.3	33.1–39.3	1.37
		Zygomatic Breadth		
D. rufulus				
Ghana (G3)	37	17.9	16.7–19.1	0.67
Ivory Coast (I2)	15	17.5	16.3–17.5	0.77
Liberia (L1)	5	17.4	17.0–17.9	0.34
Nigeria (N4)	24	18.2	17.2–19.1	0.51
D. foxi				
Nigeria (N10)	43	19.2	18.1–20.1	0.53
		Breadth of Braincase		
D. rufulus				
Ghana (G3)	37	13.4	12.9–14.3	0.31
Ivory Coast (I2)	15	13.4	12.8–14.4	0.44
Liberia (L1)	5	13.6	13.3–13.9	0.26
Nigeria (N4)	24	13.4	12.7–14.0	0.63
D. foxi				
Nigeria (N10)	43	14.1	13.6–15.0	0.34
		Breadth across Exoccipital Condyles		
D. rufulus				
Ghana (G3)	37	7.33	6.7–7.7	0.22
Ivory Coast (I2)	15	7.52	7.2–8.0	0.21
Liberia (L1)	5	7.53	7.3–7.8	0.18
Nigeria (N4)	23	7.26	6.9–7.7	0.19
D. foxi				
Nigeria (N10)	41	7.94	7.6–8.3	0.19
		Interorbital Breadth		
D. rufulus				
Ghana (G3)	37	4.40	4.0–4.8	0.16
Ivory Coast (I2)	15	4.33	4.1–4.7	0.13
Liberia (L1)	5	4.39	4.0–4.6	0.22
Nigeria (N4)	24	4.25	3.8–4.6	0.19
D. foxi				
Nigeria (N10)	43	4.51	4.2–4.9	0.15
		Length of Rostrum		
D. rufulus				
Ghana (G3)	36	9.93	8.7–11.4	0.58
Ivory Coast (I2)	13	10.42	9.6–12.3	0.75
Liberia (L1)	5	11.04	10.5–11.3	0.31
Nigeria (N4)	24	10.61	9.8–11.3	0.38

Appendix 1.—Continued.

Species and OTU	*n*	Mean	Range	*SD*
D. foxi				
Nigeria (N10)	42	11.13	10.0–12.5	0.53
		Postpalatal Length		
D. rufulus				
Ghana (G3)	37	12.03	10.9–14.2	0.72
Ivory Coast (I2)	14	11.90	10.8–13.5	0.82
Liberia (L1)	5	12.13	11.5–12.9	0.52
Nigeria (N4)	24	12.10	11.3–13.4	0.55
D. foxi				
Nigeria (N10)	41	13.08	11.3–14.9	0.73
		Length of Bony Palate		
D. rufulus				
Ghana (G3)	37	6.72	5.7–7.3	0.33
Ivory Coast (I2)	14	6.77	6.0–7.6	0.42
Liberia (L1)	5	7.07	6.5–7.7	0.54
Nigeria (N4)	24	6.98	6.4–7.5	0.29
D. foxi				
Nigeria (N10)	42	7.25	6.7–7.9	0.31
		Length of Diastemal Palate		
D. rufulus				
Ghana (G3)	37	9.96	8.9–11.7	0.58
Ivory Coast (I2)	15	9.77	8.9–11.2	0.69
Liberia (L1)	5	10.27	9.4–10.8	0.52
Nigeria (N4)	24	10.81	10.0–11.7	0.43
D. foxi				
Nigeria (N10)	43	11.32	10.1–12.5	0.56
		Length of Incisive Foramina		
D. rufulus				
Ghana (G3)	37	7.48	6.6–8.4	0.44
Ivory Coast (I2)	15	7.45	6.6–8.4	0.56
Liberia (L1)	5	7.54	7.2–8.0	0.29
Nigeria (N4)	24	7.75	7.2–8.5	0.32
D. foxi				
Nigeria (N10)	43	8.14	7.5–9.2	0.40
		Length of Auditory Bulla		
D. rufulus				
Ghana (G3)	37	5.33	5.1–5.5	0.17
Ivory Coast (I2)	15	5.21	4.9–5.5	0.19
Liberia (L1)	5	5.17	4.8–5.4	0.21
Nigeria (N4)	24	5.23	4.7–5.8	0.27
D. foxi				
Nigeria (N10)	42	5.75	5.2–6.1	0.20

Appendix 1.—Continued.

Species and OTU	*n*	Mean	Range	*SD*
		Length of Maxillary Toothrow		
D. rufulus				
Ghana (G3)	37	6.91	6.4–7.4	0.20
Ivory Coast (I2)	15	6.69	6.5–6.9	0.13
Liberia (L1)	5	6.76	6.6–7.0	0.14
Nigeria (N4)	24	6.61	6.2–7.1	0.23
D. foxi				
Nigeria (N10)	43	7.32	6.8–7.7	0.21
		Width of M1		
D. rufulus				
Ghana (G3)	37	2.33	2.1–2.5	0.08
Ivory Coast (I2)	15	2.30	2.1–2.4	0.07
Liberia (L1)	5	2.28	2.2–2.3	0.02
Nigeria (N4)	24	2.21	2.0–2.3	0.06
D. foxi				
Nigeria (N10)	43	2.52	2.3–2.7	0.08
		Total Length		
D. rufulus				
Ghana (G3)	49	260	222–313	18.8
Ivory Coast (I2)	25	281	239–324	26.5
Nigeria (N4)	34	280	254–322	17.7
D. foxi				
Nigeria (N10)	47	294	257–328	18.7
		Tail Length		
D. rufulus				
Ghana (G3)	49	122	102–146	9.6
Ivory Coast (I2)	26	138	108–158	12.7
Nigeria (N4)	34	131	114–161	10.0
D. foxi				
Nigeria (N10)	46	136	121–155	8.7
		Hindfoot Length		
D. rufulus				
Ghana (G3)	50	32.2	30–35	1.2
Ivory Coast (I2)	26	32.8	30–36	1.4
Nigeria (N4)	36	31.8	27–36	2.2
D. foxi				
Nigeria (N10)	49	33.6	31–37	1.3
		Weight		
D. rufulus				
Ghana (G3)	50	76	45–125	16.0
Ivory Coast (I2)	26	77	44–116	19.6
Nigeria (N4)	36	82	61–116	14.9
D. foxi				
Nigeria (N10)	49	118	73–174	23.9

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 436–447

A NEW SPECIES OF FROG OF THE *ELEUTHERODACTYLUS LACRIMOSUS* ASSEMBLY FROM AMAZONIA, SOUTH AMERICA (AMPHIBIA: ANURA: LEPTODACTYLIDAE)

W. Ronald Heyer and Laura M. Hardy

Abstract.—*Eleutherodactylus zimmermanae,* new species, is described from the Amazon Basin of South America. Because of the biological and nomenclatural complexity of frogs of the *Eleutherodactylus lacrimosus* assembly, a neotype is designated for *Cyclocephalus lacrimosus* Jiménez de la Espada, 1875.

Barbara Zimmerman has studied the ecology of frogs as part of the Biological Dynamics of Forest Fragments Project initiated by the Instituto Nacional de Pesquisas da Amazônia (INPA) and the World Wildlife Fund (WWF). This project was originally named the Minimum Critical Size of Ecosystems Project and is now co-administered by the Smithsonian Institution's (SI) National Museum of Natural History. Zimmerman has been involved with research on frogs at the study sites north of Manaus, Amazonas, Brazil, since almost the inception of the project some ten years ago (for further information, see Zimmerman & Rodrigues 1990). Zimmerman has collected three species of *Eleutherodactylus* from the INPA-WWF-SI research sites. She has identified one of these as *E. fenestratus,* but was unable to identify the other two and referred to them as species "1" and "2" (Zimmerman & Rodrigues 1990). Material of the *Eleutherodactylus fenestratus-guttur-alis* complex from the INPA-WWF-SI sites seems to represent a single species that embraces the throat patterns used to distinguish *gutturalis* from *fenestratus* (Hoogmoed et al. 1977). Further study of all available materials of this complex is required to determine which name properly applies to the species at the INPA-WWF-SI sites. The species Zimmerman referred to as "2" (Zimmerman & Rodrigues 1990) we identify as *Eleutherodactylus ockendeni.* The species she referred to as "1" is a new species allied to what Lynch & Schwartz (1971) and Lynch (1980) called *Eleutherodactylus lacrimosus,* which we describe as:

Eleutherodactylus zimmermanae,
new species
Figs. 1, 2, 3

Holotype.—MZUSP 64539, adult male from Brazil: Amazonas, Reservas INPA-WWF-SI, approximately 80 km N of Manaus, approximately 2°20′S, 59°50′W. Collected by Barbara Zimmerman, 7 Dec 1984.

Paratopotypes.—INPA 1371, MZUSP 64535–38, 64540–41, USNM 304278–304279, collected by Barbara Zimmerman on 7 Dec 1984 (MZUSP 64535-38) and 17 Mar 1987 (remainder of paratopotypes).

Methodological note.—The morphological terminologies and definitions used herein follow those detailed in Heyer et al. (1990) in general and Savage (1987) for finger and toe tips.

Diagnostic definition (scheme established by Lynch, e.g., 1979, of numbered character states followed here for ease of comparison).—(1) Skin of upper surfaces generally smooth, that of venter coarsely areolate; (2) tympanum distinct, its horizontal diameter about ⅓ eye diameter; (3) snout subelliptical with pointed tip in dorsal view, acute in

Fig. 1. Specimens photographed in life by Walter Hödl from Reserva Ducke, Amazonas, Brazil. Above, single male NMW 32112:1, below, amplectant pair NMW 32112:2–3.

Fig. 2. Dorsal view of holotype of *Eleutherodactylus zimmermanae,* MZUSP 64539, adult male.

profile; canthus rostralis sharply rounded; (4) upper eyelid width slightly smaller than interocular distance, with several well defined tubercles; no cranial crests; (5) no vomerine teeth; (6) males with vocal slits and single subgular vocal sac expanded and wrinkled in preservation; no nuptial asperities on thumb; (7) first finger just shorter than second; fingers bearing large disks (largest on III and IV); disks broader than long; (8) fingers with weakly to well-developed lateral keels; (9) row of two to five distinct ulnar tubercles; (10) row of three to four fleshy tubercles on inner tarsus, but no fold (usually); heel smooth to granular; (11) two metatarsal tubercles, inner oval, two to three times size of outer; a few scattered fleshy plantar tubercles; (12) toes bearing weakly to well-developed lateral keels; no webbing; toe disks about same size as those of outer fingers; (13) predominantly brown frog, no flash colors; posterior surface of thighs brown; (14) adults small, males 19.1–21.2 mm, females 22.4–25.8 mm SVL.

Throughout most of its range, *E. zimmermanae* occurs with *E. fenestratus* and *E. ockendeni. Eleutherodactylus fenestratus* has a smooth belly; the belly is areolate in *E. zimmermanae. Eleutherodactylus ockendeni* lacks ulnar and tarsal tubercles and usually has distinct dark suborbital bars; *E. zimmermanae* has ulnar and tarsal tubercles and suborbital bars, if present, are faint. See Discussion for additional diagnostic comparisons.

Description of holotype.—Snout shape

subelliptical and pointed at tip in dorsal outline, acute in profile; canthus rostralis sharply rounded; lip barely flared; upper eyelid width slightly less than interocular distance; no external indications of cranial crests; tympanum hidden by supratympanic fold dorsally, distinct and somewhat flared below, small, horizontal diameter about ⅓ eye diameter; no vomerine teeth; choanae small, bean-shaped, separated by distance three to four times diameter of single choana; vocal slits present, elongate; vocal sac single, distended, extending to chest region; finger lengths I just < II < IV < III; finger disks present, smallest on thumb ovoid, Finger II disk also ovoid but larger, disks on Fingers III and IV largest, broadened, upper surfaces not indented or notched, largest disk about same size as tympanum; fingers with weak lateral keels; finger webbing absent; single fleshy tubercle on outer edge of hand nearer finger than base of palm; palmar tubercle large, bifid, about twice size of ovate thenar tubercle, supernumerary palmar tubercles not obvious; subarticular tubercles distinct, rounded, single; nuptial excrescences absent; outer ulnar region with row of three pale rounded fleshy tubercles; supratympanic fold weakly developed; other glands or folds on top or sides of body absent; upper eyelid with several tubercles, rest of dorsum smooth except scattered, weakly developed tubercles on dorsal surface of shank; throat smooth, vocal sac wrinkled; fold distinct between chest and belly; posterior chest and entire belly areolate-granular; ventro-posterior surfaces of thighs weakly granular; ventral limb surfaces smooth; toe lengths I < II < III < V < IV; disk on Toe I very small, barely broader than toe; disks on Toes II and III ovoid and increasingly larger; disks on Toes IV and V large, broadened, largest toe disks slightly larger than largest finger disks; sides of toes with weak keels; barest rudiment of webbing between Toes IV–V, otherwise webbing absent; outer round metatarsal tubercle about ⅓ size of ovate inner metatarsal tubercle; series of three relatively evenly spaced, rounded, fleshy tubercles along tarsus (but no fold); remainder of outer tarsal region smooth; heel smooth; plantar surface with a few scattered indistinct rounded fleshy tubercles; subarticular tubercles distinct, rounded.

Fig. 3. Side of head of holotype of *Eleutherodactylus zimmermanae.*

Coloration in alcohol: Tip of snout, incomplete canthal stripe, distinct interorbital bar, and supratympanic fold dark brown; tympanum and side of head weakly mottled with brown and tan, faint suborbital bars; area in front of interorbital bar pale tan with indistinct small brown flecks; dorsum with faint brown W in scapular region; remainder of back with broken dark stripes and two transverse series of dots between sacrum and vent; otherwise dorsum with relatively densely scattered melanophores; flanks with series of oblique incomplete dark brown stripes; upper surfaces of limbs with dark wrist stripes and remainder of upper limbs, except for shanks, with darker brown transverse bars on a lighter brown background, cross bars incomplete on upper surfaces of shanks; ventral surfaces of limbs with scattered melanophores; unpigmented on posteriormost part of belly and on upper thighs; posterior surfaces of thighs with scattered, evenly distributed brown melanophores.

Measurements of holotype.—SVL 19.1 mm, head length 7.2 mm, head width 6.9 mm, horizontal tympanum diameter (in-

cluding annulus) 0.9 mm, thigh 8.4 mm, shank 9.5 mm, foot 8.0 mm.

Variation.—Only features that extend the variation beyond that given for the holotype are presented.

SVL for other males examined (n = 12) 19.6–21.6 mm SVL, females (n = 6) 22.3–25.8 mm SVL; head length 37–40% SVL (males and females); head width 33–38% SVL (males), 38–40% SVL (females); tympanum horizontal diameter 4–6% SVL (males and females); thigh length 42–48% SVL (males and females); shank length 46–51% SVL (males and females); foot length 41–45% SVL (males and females).

Dorsal outline of snout subelliptical or subovoid, usually strongly pointed at tip, weakly pointed at tip in one individual; snout profile rarely weakly acute; choanal shape sometimes ovate; first finger rarely about same length as second; disks on Fingers I and II sometimes ovoid-broadened, sometimes broadened on II, disk on III with barest dorsal medial indentation in one individual, largest disks rarely larger than tympanum; finger edges sometimes distinctly keeled; short dermal fold on edge of hand continuous or not with outer finger ridge, sometimes reduced to single elongate to rounded fleshy tubercle; palmar tubercle ranging in size to about same as thenar tubercle, palmar tubercle usually deeply bifid; four prominent to indistinct fleshy round supernumerary palmar tubercles; from two to five (usually four) fleshy tubercles on outer ulnus (sometimes only indicated by light spots apparently due to preservation artifact); dorsum in some with scattered, weakly developed tubercles, dorsal tubercles much less obvious than eyelid tubercles; upper flanks sometimes with scattered tubercles or entire flanks sometimes weakly granular; dorsal tubercles on shank indistinct in some specimens; discoidal fold at anterior belly well developed to absent; belly in some specimens irregularly areolate; disk on Toe I usually noticeably broader than toe, ovoid, disk on Toe III also ovoid-broadened to broadened; largest toe disks also same size as or slightly smaller than largest finger disks; toes in some specimens with distinct lateral keels; no vestige of toe webbing in some specimens; outer metatarsal tubercles ranging in size from ⅓ to almost ½ size of inner; some individuals with row of four fleshy tubercles on outer tarsus (tubercles in some only discernible by light spots apparently due to preservation artifact), in two specimens a tarsal fold evident with two to three weak to prominent tubercles on it; two to three other fleshy tubercles scattered on outer tarsal surface (smaller than tubercles in tarsal fold zone) in some specimens; heel sometimes granular or with two to three low fleshy tubercles; in addition to fleshy tubercles, plantar surfaces granular in some specimens; two small, light, fleshy, tubercles in metatarsal fold region near toe in some specimens, such tubercles, if present, always smaller than outer hand tubercles on any given specimen; in one individual, three additional less distinct tubercles in proximal metatarsal fold area, but not on same line with two tubercles in distal metatarsal fold area.

Tip of snout not darker than surrounding pattern in some specimens; canthal stripe ranging from well defined to absent, but usually apparent; side of head uniform brown in some individuals; interorbital bar narrow, or interrupted, or abutting light bar anteriorly in some individuals; snout anterior to interorbital bar ranging from noticeably lighter to same intensity as dorsal ground color; dorsal pattern variable, including broad scapular chevron continuous with dark interorbital triangle extending posteriorly from interorbital bar, vaguely defined broad sacral chevron, dark transverse band anterior to vent, broad scapular W-shaped mark more distinct than described for holotype in some specimens, two broad but ill-defined lighter dorsolateral bands from eyes to mid-flanks in some in-

dividuals, or dorsum almost uniform with two lines of dots behind eyes in others; upper surfaces of limbs sometimes indistinctly striped to almost uniform tan; oblique stripes on flanks sometimes barely defined to an indistinct scattering of darker brown dots on a brown ground color; posterior surfaces of thighs sometimes uniform brown or with lighter areas distally.

WCAB 2315 from Serra do Navio, Amapá, Brazil, is somewhat distinctive in having well-developed tarsal folds with three swellings (in same places as tubercles in other specimens). The ulnar tubercles are the same as in other specimens.

Three specimens from Colombia (KU 153286–153288) differ from other specimens in that the ulnar and tarsal tubercles are ill-defined at best and the dark dorsal markings are sharply defined. These specimens should be re-evaluated in any further taxonomic considerations dealing with Colombian members of the *lacrimosus* assembly.

Color in life.—Type specimens collected 17 Mar 1987: "Iris copper with darker reddish streak running across eye horizontally. Irises of two specimens are more reddish brown than copper. Copperish sheen on back and snout. Dorsal colouration varies among the three individuals. Two individuals have distinct interorbital yellow line that divides a reddish snout from darker brown dorsum. All three specimens have unmarked yellow throats and venters. All three have some dark markings on back but form of markings varies" (B. L. Zimmerman field notes, pers. comm.).

Rondônia specimens: "Dorsum light brown. Triangle of darker brown from eyes and extending to middle of back. Triangle outlined with lighter yellow-brown line. Venter lighter yellow-brown. Stripes of black on chest and chin. Eye yellow brown with light orange stripe. Black reticulations in eye [MZUSP 61551]. Dorsum patterned with tan and brown. Light tan triangular area from snout to between eyes. Eyes pale bronze with reddish streak [MZUSP 61553]. Yellow thighs [MZUSP 61554]. Pale salmon-colored thighs [MZUSP 61555]" (J. P. Caldwell field notes, pers. comm.). "Medium brown above with darker, vague scapular W. Dark interorbital line; snout anterior to it pale tan. Eyelids and postocular stripes slightly darker tan. Entire venter dull yellow but throat bright lemon yellow. Concealed thighs dull orange-yellow. Iris brassy [USNM 304166]" (R. I. Crombie field notes, pers. comm.).

Advertisement call.—Call a sharp "té" chirp; no call groups (based on analyses of 50 sec segments at beginning, middle, and end of 306 sec tape); based on loudest calls, maximum call rate 1.03 calls/sec; call duration about 0.05 sec (exact duration undeterminable due to background calls blending with loudest calls); one markedly to weakly pulsatile note/call, about 18 pulses/call given at a rate of 340 pulses/sec; call moderately intensity modulated, first half of call louder than second; call markedly frequency modulated, starting at lowest frequency of call and rising quickly to highest frequency; average (of 33 calls) frequency sweep 3485–4222 Hz; frequency shift in maximal energy of call from beginning to end of tape 4000 to 3500 Hz; dominant frequency same as fundamental; no harmonic structure evident in call (Fig. 4).

Etymology.—Named for Barbara Zimmerman in recognition of her contributions toward an understanding of Amazonian frogs.

Ecological notes.—"A widespread and commonly heard species throughout the forest. Calls exclusively nocturnally from 1.5–2.5 meters high especially in shrubby, tangled, or treefall type of vegetation. Generally 1 to 5 males call in a group. They call more in the wetter months, mostly from November until May. During the month of peak calling activity, the average abundance of calling males is eleven per km [of trail],

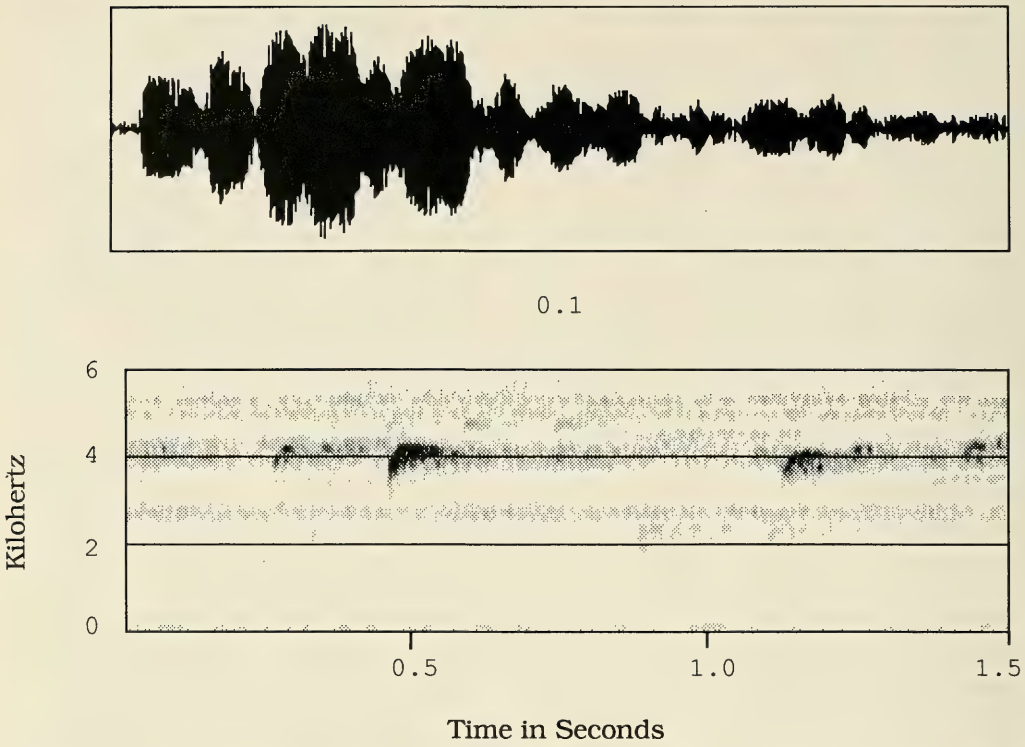


Fig. 4. Wave form and audiospectrogram of advertisement call of *Eleutherodactylus zimmermanae.* From recording USNM tape 154, cut 2, recorded by B. L. Zimmerman on 07 December 1984, 2012 h.

falling to less than one caller per km during the driest month. They are extremely hard to find although the call is clearly heard" (B. L. Zimmerman notes from INPA-WWF-SI sites, pers. comm.).

Walter Hödl collected a pair in amplexus (Fig. 1, below) at the Reserva Ducke, Amazonas (NMW 32112:2–3) at 2115 h on 10 Mar 1990 on a leaf of a bush at a height of 1.7 m. From the same locality, he recorded and collected a calling male (NMW 32112: 1) (Fig. 1, above) at 2050 h on 13 Mar 1990 on a tree at a height of about 2 m during a slight rain.

Janalee P. Caldwell recorded the following information on a series collected from Santa Cruz da Serra, Rondônia: (a) in rolled up leaf of plant (3′) in forest during day, 15 May 1985 (MZUSP 61550); (b) from relatively undisturbed forest, in center of banana plant after all leaves removed, wedged in axil of last leaf, 1400 h, 15 May 1985 (MZUSP 61551); (c) from a bromeliad on a fallen tree, about 1200 h, 6 Jun 1985 (MZUSP 61552); (d) on a bromeliad on a fallen log near a drying pond at night, 2 Sep 1985 (MZUSP 61553); (e) in a large bromeliad in a log in a pond by the road, about 1600 h, 7 Sep 1985 (MZUSP 61554–61555).

Ronald I. Crombie captured two calling males, one from Alto Paraiso, Rondônia (USNM 304166), 3 m up on a stem of a small tree in degraded forest at night on 29 Oct 1985, and one from Santa Cruz da Serra (USNM 304167) on a leaf 2.5 m up on a small tree in good forest at night on 6 Nov 1985. (See Vanzolini, 1986, for discussion of Rondônia localities.)

Referred specimens.—BRAZIL. ACRE: Estrada Rio Branco-Abunã, 90 km from Rio Branco, MZUSP 6532. AMAPÁ: Serra do Navio, WCAB 2315. AMAZONAS: Reser-

Fig. 5. Northern South America known distribution of *Eleutherodactylus zimmermanae*. Square = type locality. Dots = other localities.

va Ducke, MZUSP 50164, NMW 32112:1–3. RONDÔNIA: Alto Paraiso, USNM 304166; Santa Cruz da Serra, MZUSP 61550–61555, USNM 304167.

COLOMBIA. AMAZONAS: Petuna, Río Loreto-yacu, KU 153286–153288.

Note: We specifically restrict the types to the specimens collected from the type locality.

Distribution.—Known from a few scattered localities in the Amazon Basin (Fig. 5).

As far as is known, *E. lacrimosus* occurs only on the eastern Andean slope region of Ecuador. We have examined the Brazilian and Colombian specimens identified by Lynch & Schwartz (1971) as *E. lacrimosus*. Our opinions about these specimens are the following. WCAB 2315 from Serra do Navio, Brazil is *E. zimmermanae*. KU 127318 from near Belém, Brazil appears to represent a different (probably new) species of the *lacrimosus* assembly. Although the specimen is somewhat desiccated, a distinct rudimentary web between Toes IV and V distinguishes this specimen from both *E. lacrimosus* and *E. zimmermanae*. KU 110410 from Isla la Vieja, Caquetá, Colombia, also is neither *E. lacrimosus* nor *E. zimmermanae*; it has vomerine teeth and a distinct tarsal fold bearing two to three tubercular projections. Of the described members of the *lacrimosus* assembly, this specimen seems to be closest to *E. petersi* (but see the comment on *E. petersi* in the following discussion).

Discussion

Eleutherodactylus zimmermanae is a member of the *E. lacrimosus* assembly of

the *E. unistrigatus* group as defined by Lynch & Duellman (1980). The *lacrimosus* assembly as used by Lynch applied herein is a phenetic subgroup within the large *E. unistrigatus* species group. Lynch & Ruíz-Carranza (1985) indicated that the species belonging to the *lacrimosus* assembly were: *boulengeri, brevifrons, bromeliaceus, eremitus, lacrimosus, mendax, petersi, phoxocephalus, prolixodiscus,* and *tayrona.* Subsequently, Rivero & Serna (1987) added *E. dorsopictus* and Duellman (1990) added *E. schultei* to the assembly. Lynch (pers. comm.) suggested that *E. apiculatus* Lynch & Burrowes (1990) is part of this assembly, but based on our reading of the description, *E. apiculatus* seems quite distinct from other assembly members. It should be pointed out that Lynch (in litt., 9 Jan 1991) views his "*lacrimosus* assembly as a phenetic unit rather than a taxonomic one" perhaps representing "consequences of life between the axils of bromelias." The nomenclature of *E. lacrimosus* and the variation in systematic characters separating these taxa preclude a straightforward comparison and distinction of *E. zimmermanae* from the other members of the assembly.

Cyclocephalus lacrimosus Jiménez de la Espada (1875) is based on an illustration of the dorsal view and line drawings of the pectoral girdle and open mouth (Plate 3 bis, figures 5, 5a, 5b); no description accompanied the drawings. William E. Duellman did not find the type in the Madrid collection during a search for Jiménez de la Espada types (Lynch & Schwartz 1971:107). Frost (1985:298) gave the type status as "Lost." We asked the curator at the Museo Nacional de Ciencias Naturales, Madrid, whether the type had been located since Duellman had examined the collection. In spite of further searching efforts, the type has not been found (José Enrique González Fernández, in litt., 24 Oct 1990). Most of the collection that included the type of *Cyclocephalus lacrimosus* perished after reaching Spain (Savage 1978:xii); all evidence indicates that the type of *Cyclocephalus lacrimosus* has been lost or destroyed.

Lynch & Schwartz (1971) concluded that Espada's figures were sufficient to associate the name with museum specimens of (what they considered to be) a rather wide-ranging Amazonian species of *Eleutherodactylus,* for which they provided a new diagnosis, description, and figure of the dorsum. Lynch & Schwartz (1971:110) interpreted nine features from the figures: "(1) skin of dorsum finely shagreened; (2) digits bearing small digital pads; (3) digits free of webbing; (4) first finger nearly as long as second; (5) prevomerine dentigerous processes present, sharply inclined; (6) omosternum small; (7) posterior surface of thigh unicolor; (8) color pattern simple; and (9) outline of head in form of half circle." We do not find the figure copies available to us adequate to determine whether the dorsal texture is smooth or finely shagreened. Only one hand is figured; because of the perspective, the first finger could be considerably shorter than the second. The outline of the head of the type figures is indeed a half circle with no indication of a pointed snout tip (papilla) characteristic of members of the *E. lacrimosus* assembly. In 1971, Lynch & Schwartz thought there was a single species in what is now an assembly of eleven species. We believe that there is not enough information extractable from Jiménez de la Espada's figures to associate absolutely his *lacrimosus* with only one of the species within the *E. lacrimosus* assembly.

The species that Lynch & Schwartz redescribed and figured as *lacrimosus* is the most distinctive species within the assembly; it has smooth upper eyelids and lacks series of ulnar and tarsal tubercles, all features found to varying degrees in the other members of the assembly. Because Lynch & Schwartz's (1971) redescription has been used by all subsequent workers to define *E. lacrimosus* and because there is sufficient

doubt (in the absence of a type) as to the exact allocation of Jiménez de la Espada's *Cyclocephalus lacrimosus,* we think the situation merits designation of a neotype to preclude further confusion. We have examined and hereby designate KU 110782, an adult female from Santa Cecilia, Napo, Ecuador, 340 m (the specimen figured by Lynch & Schwartz 1971: fig. 4), as the neotype of *Cyclocephalus lacrimosus.* The neotype conforms to the description provided by Lynch & Schwartz (1971) with the minor exceptions that the upper eyelids, although flattened in preservative, appear to be weakly tuberculate and moderately developed antebrachial tubercles are present. The neotype is from the region known to have been visited by Jiménez de la Espada (Savage 1978).

Eleutherodactylus zimmermanae occurs in the lowlands of Amazonia. All other known members of the *E. lacrimosus* assembly occur on moderate to high slopes of the Andes in Colombia, Ecuador, and Peru. However, the closely related *E. tubernasus* assembly occurs in Venezuela (Lynch & Ruíz-Carranza (1985). Preserved members of the *E. lacrimosus* assembly almost need to be compared side by side with each other to differentiate the species. In many instances, the development of tubercles and color patterns is distinctive, but it is difficult to express those differences adequately in words. Of the described species of the *E. lacrimosus* assembly, only *E. dorsopictus, E. mendax, E. zimmermanae,* and some individuals of *E. brevifrons* and *E. schultei* lack vomerine teeth. *Eleutherodactylus brevifrons* has pale green upper eyelids in life and is known from several localities in the high cloud forests of the Cordillera Occidental and the north part of the Cordillera Central of Colombia (J. D. Lynch, pers. comm.). *Eleutherodactylus mendax* from the Andean slopes of Amazonian Peru has smooth heels and a green dorsum in life. *Eleutherodactylus zimmermanae* does not have a green dorsum in life and usually has granular or fleshy tuberculate heels. *Eleutherodactylus schultei,* from high elevation cloud forest in the northern part of the Cordillera Central, Department of Amazonas, Peru, lacks eyelid tubercles and is larger than *E. zimmermanae* (*E. schultei*—males 23.5–26.6 mm, females 28.4–34.0 mm SVL). *Eleutherodactylus dorsopictus* from the Páramo de Sonsón, Cordillera Central, Colombia, has divided subarticular tubercles on the hand; in *E. zimmermanae* the subarticular tubercles are single.

We are aware of at least two other new species in this assembly being worked on by others. Once variation in this assembly is better understood, more species will be recognized from specimens already in collections. For example, the paratypes of *E. petersi* in the USNM collections apparently represent two species in addition to *petersi.*

Most members of the *E. lacrimosus* assembly are associated with or at least often collected from bromeliads (Lynch & Schwartz 1971; Duellman 1978a, 1990; Lynch 1978, 1979, 1980, 1981; Lynch & Duellman 1980; Lynch & Ruíz-Carranza 1985; Rivero & Serna 1987), but *E. apiculatus* is not associated with bromeliads (Lynch & Burrowes 1990). *Eleutherodactylus zimmermanae* may demonstrate differential use of bromeliads depending on their abundance or season of the year. J. P. Caldwell found them in bromeliads in Rondônia, but R. I. Crombie did not. B. Zimmerman did not notice an association with bromeliads in the central Amazon Basin.

Calls have been noted for seven other species of the assembly (none of which have been recorded). The calls of *E. boulengeri, brevifrons, lacrimosus,* and *petersi* are described as single "peeps" (Duellman 1978b, Lynch & Duellman 1980, Lynch 1981), *E. phoxocephalus* as a single sharp whistle (Lynch 1979), *E. schultei* as "ping-ping" (Duellman 1990), and *E. apiculatus* as "peeep-peeep" (Lynch & Burrowes 1990).

Perhaps recordings of members of this assembly will help in establishing the boundaries of the species limits.

Acknowledgments

Research for this paper was initiated while Laura M. Hardy was a Smithsonian Institution Natural History Summer Intern.

Barbara Zimmerman made her data from the INPA-WWF-SI research sites available to us. Janalee P. Caldwell, Ronald I. Crombie, and Walter Hödl also shared their field data with us. Werner C. A. Bokermann (WCAB), W. E. Duellman, University of Kansas Museum of Natural History (KU), F. Tiedemann, Naturhistorisches Museum Wien (NMW), and P. E. Vanzolini, Museu de Zoologia da Universidade de São Paulo (MZUSP) allowed us to examine specimens in their care. José Enrique González Fernández kindly searched the Museo Nacional de Ciencias Naturales collection for the type of *Cyclocephalus lacrimosus*. Ronald I. Crombie and John D. Lynch critically read drafts of this paper. Jennifer Westhoff drew the illustrations reproduced as Figs. 2 and 3. Walter Hödl allowed us to use his slides to produce Fig. 1.

Research leading to this paper was supported, in part, by the Museu de Zoologia da Universidade de São Paulo and the IESP Neotropical Lowland Research Program, Smithsonian Institution. Mr. Adam Zimmerman donated the funds for printing the color plate which enhances this paper.

Literature Cited

Duellman, W. E. 1978a. Three new species of *Eleutherodactylus* from Amazonian Perú (Amphibia: Anura: Leptodactylidae).—Herpetologica 34: 264–270.

———. 1978b. The biology of an equatorial herpetofauna in Amazonian Ecuador.—University of Kansas Museum of Natural History, Miscellaneous Publication 65:1–352.

———. 1990. A new species of *Eleutherodactylus* from the Andes of northern Peru (Anura: Leptodactylidae).—Journal of Herpetology 24:348–350.

Frost, D. R. (ed.). 1985. Amphibian species of the world. Allen Press, Inc., and The Association of Systematic Collections, Lawrence, Kansas, 732 pp.

Heyer, W. R., A. S. Rand, C. A. G. da Cruz, O. L. Peixoto, & C. E. Nelson. 1990. Frogs of Boracéia.—Arquivos de Zoologia 31:231–410.

Hoogmoed, M. S., J. D. Lynch, & J. Lescure. 1977. A new species of *Eleutherodactylus* from Guiana (Leptodactylidae, Anura).—Zoologische Mededlingen 51:33–41.

Jiménez de la Espada, M. 1875. Vertebrados del Viaje al Pacífico Verificado de 1862 a 1865 por una Comisión de Naturalistas enviada por el Gobierno Español. Batracios. Imprenta de Miguel Ginesta, Madrid, 208 pp.

Lynch, J. D. 1978. A new eleutherodactyline frog from the Andes of northern Colombia (Leptodactylidae).—Copeia 1978:17–21.

———. 1979. Leptodactylid frogs of the genus *Eleutherodactylus* from the Andes of southern Ecuador.—University of Kansas Museum of Natural History, Miscellaneous Publication 66:1–62.

———. 1980. *Eleutherodactylus eremitus*, a new trans-Andean species of the *lacrimosus* assembly from Ecuador (Amphibia: Leptodactylidae).—Museum of Comparative Zoology Breviora 462: 1–7.

———. 1981. Two new species of *Eleutherodactylus* from western Colombia (Amphibia: Anura: Leptodactylidae).—Occasional Papers of the Museum of Zoology, University of Michigan 697:1–12.

———, & P. A. Burrowes. 1990. The frogs of the genus *Eleutherodactylus* (Family Leptodactylidae) at the La Planada Reserve in southwestern Colombia with descriptions of eight new species.—Occasional Papers of the Museum of Natural History, University of Kansas 136:1–31.

———, & W. E. Duellman. 1980. The *Eleutherodactylus* of the amazonian slopes of the Ecuadorian Andes (Anura: Leptodactylidae).—University of Kansas Museum of Natural History, Miscellaneous Publication 69:1–86.

———, & P. M. Ruíz-Carranza. 1985. A synopsis of the frogs of the genus *Eleutherodactylus* from the Sierra Nevada de Santa Marta, Colombia.—Occasional Papers of the Museum of Zoology, University of Michigan 711:1–59.

———, & A. Schwartz. 1971. Taxonomic disposition of some 19th Century leptodactylid frog names.—Journal of Herpetology 5:103–114.

Rivero, J. A., & M. A. Serna. 1987. Tres nuevas especies de *Eleutherodactylus* (Amphibia, Leptodactylidae) de Antioquia, Colombia.—Caribbean Journal of Science 23:386–399.

Savage, J. M. 1978. Marcos Jiménez de la Espada,

naturalist explorer of the Andes and upper Amazon Basin. Pages vii–xvi in reprinted edition of Vertebrados del Viaje al Pacifico. Batracios.—Society for the Study of Amphibians and Reptiles.

———. 1987. Systematics and distribution of the Mexican and Central American rainfrogs of the *Eleutherodactylus gollmeri* group (Amphibia: Leptodactylidae).—Fieldiana: Zoology, New Series 33:1–57.

Vanzolini, P. E. 1986. Levantamento herpetológico da área do estado de Rondônia sob a influência da rodovia BR 364.—Programa Polonoroeste, Relatório de Pesquisa 1:1–50.

Zimmerman, B. L., & M. T. Rodrigues. 1990. The frogs, snakes, and lizards of the INPA-WWF reserves near Manaus in the central Amazon. Pp. 426–454 *in* A. Gentry, ed., Four neotropical rainforests. Yale University Press, New Haven.

(WRH) Division of Amphibians and Reptiles, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (LMH) 1823 S. Brookwood Dr., Shreveport, Louisiana 71118.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 448–458

SYMPHURUS PROLATINARIS, A NEW SPECIES OF SHALLOW-WATER TONGUEFISH (PLEURONECTIFORMES: CYNOGLOSSIDAE) FROM THE EASTERN PACIFIC

Thomas A. Munroe, Martha S. Nizinski, and M. N. Mahadeva

Abstract.—*Symphurus prolatinaris* is described from 201 specimens collected in shallow waters on the continental shelf (9–162 m, 96% taken between 13 and 42 m) from northern Mexico to central Peru. A medium-sized tonguefish, *S. prolatinaris* attains maximum lengths of 161 mm SL, with females maturing at ca. 98 mm SL. The new species is characterized by a predominant 1-5-3-2-2 pattern of interdigitation of dorsal pterygiophores and neural spines; 12 caudal-fin rays; 102–112 dorsal-fin rays; 85–93 anal-fin rays; 54–58 total vertebrae; four hypurals; a lightly-pigmented, triangular, veil-like pupillary operculum; 3–8 small, ctenoid scales on the blind sides of dorsal- and anal-fin rays; a pronounced, tubular, anterior nostril on the blind side; the first dorsal-fin ray located anterior to a vertical through the front margin of the upper eye; and the ocular-side lower jaw without a pronounced fleshy ridge on its posterior extent. *Symphurus prolatinaris* is most similar to *S. chabanaudi* Mahadeva & Munroe, but differs notably from that species in possessing a pupillary operculum, in pigmentation, and in its more anteriorly placed dorsal fin.

Recent studies of symphurine tonguefishes occurring in warm temperate and tropical neritic waters of the eastern Pacific Ocean (Munroe & Mahadeva 1989, Mahadeva & Munroe 1990, Munroe & Nizinski 1990) indicate that tonguefishes of the genus *Symphurus* are considerably more diverse in this region than previously reported (Meek & Hildebrand 1928, Hildebrand 1946, Mahadeva 1956, Chirichigno 1974). To date, over 17 nominal species have been described from eastern Pacific locations, and the examination of tonguefishes collected in relatively shallow waters between northern Mexico and Peru has revealed yet another undescribed species from this area.

In his dissertation, Mahadeva (1956:172) examined a tonguefish specimen (LACM 20406) that he was unable to identify. This specimen had counts comparable to those of an undescribed species, later described as *S. chabanaudi* Mahadeva & Munroe, 1990, but differed from that species in body pigmentation, in possessing a thin, veil-like pupillary operculum (absent in *S. chabanaudi*), in features of its gill-arch morphology, and in the more-anteriorly placed dorsal-fin. Noting the differences between this specimen and those of *S. chabanaudi,* Mahadeva was unable to positively identify this specimen and he listed it as incertae sedis.

Since Mahadeva's study (1956), significant collections of tonguefishes have been made throughout eastern Pacific coastal seas from Mexico to northern South America. From this material, we now have identified an additional 200 specimens matching characteristics of the incertae sedis specimen listed in Mahadeva's study and have determined that these specimens represent

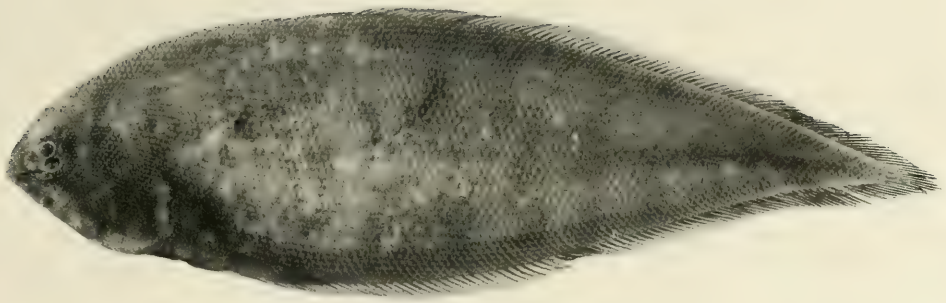


Fig. 1. *Symphurus prolatinaris,* new species, holotype, USNM 308408, male, 112.8 mm SL; Colombia, 4°20′–4°18′N, 77°28′–77°29′W.

an undescribed species. A formal description of the new species is presented at this time.

Methods.—Type and non-type specimens of the new species are deposited in the following institutions: California Academy of Sciences (CAS); National Museum of Natural History (USNM); Natural History Museum of Los Angeles County (LACM); Scripps Institution of Oceanography, Marine Vertebrate Collection (SIO); University of California at Los Angeles (UCLA); University of Arizona (UA); Instituto del Mar del Peru (IMARPE); and Universidad de Costa Rica, Museo de Zoologia (UCR).

Counts and measurements follow Munroe & Mahadeva (1989) and Munroe (1990). Standard length (SL) is used throughout. Morphometric ratios are expressed in thousandths of SL or thousandths of head length. Abbreviations are: ID pattern—interdigitation pattern of dorsal pterygiophores and neural spines; BD—body depth; PAL—preanal length; CFL—caudal-fin length; PL—pelvic-fin length; DBL—dorsal-fin length; PDL—predorsal length; ABL—anal-fin length; HL—head length; HW—head width; POL—postorbital length; UHL—upper head lobe width; LHL—lower head lobe width; SNL—snout length; UJL—upper jaw length; ED—eye diameter; CD—chin depth.

All descriptions of pigmentation are based on fish fixed in formalin and stored in ethyl or isopropyl alcohol. Size at maturity was estimated by macroscopic examination of the extent of posterior elongation of the ovaries (ovaries of mature females are often conspicuous through the body wall when light is transmitted from beneath the specimen; in immature females, developing ovaries are best observed by dissection). Since no obvious differences in testicular size were apparent in males, estimates of maturity were based entirely on females. Depth of capture (in feet or fathoms) was transformed to the nearest meter. If depth included a range of depths over which the nets were towed, an average depth for that particular trawl was calculated.

Symphurus prolatinaris, new species

Figs. 1, 2a, 3–4, Tables 1–3

Holotype.—USNM 308408 (male, 112.8 mm); Colombia, off Rio Togoroma, 4°20′–4°18′N, 77°28′–77°29′W, 9 m, 6 Nov 1970. Collected by L. Knapp with 50 ft shrimp trawl, R/V *Inderena,* Cruise 7010, Station 344.

Paratypes.—(Measured and counted 24 specimens; 103.8–161 mm): Mexico.—SIO 65-158 (2, 123.2–129.2), Sinaloa, Isla Altamura, 24°37.5′N, 108°13.5′W, 27 m, 26

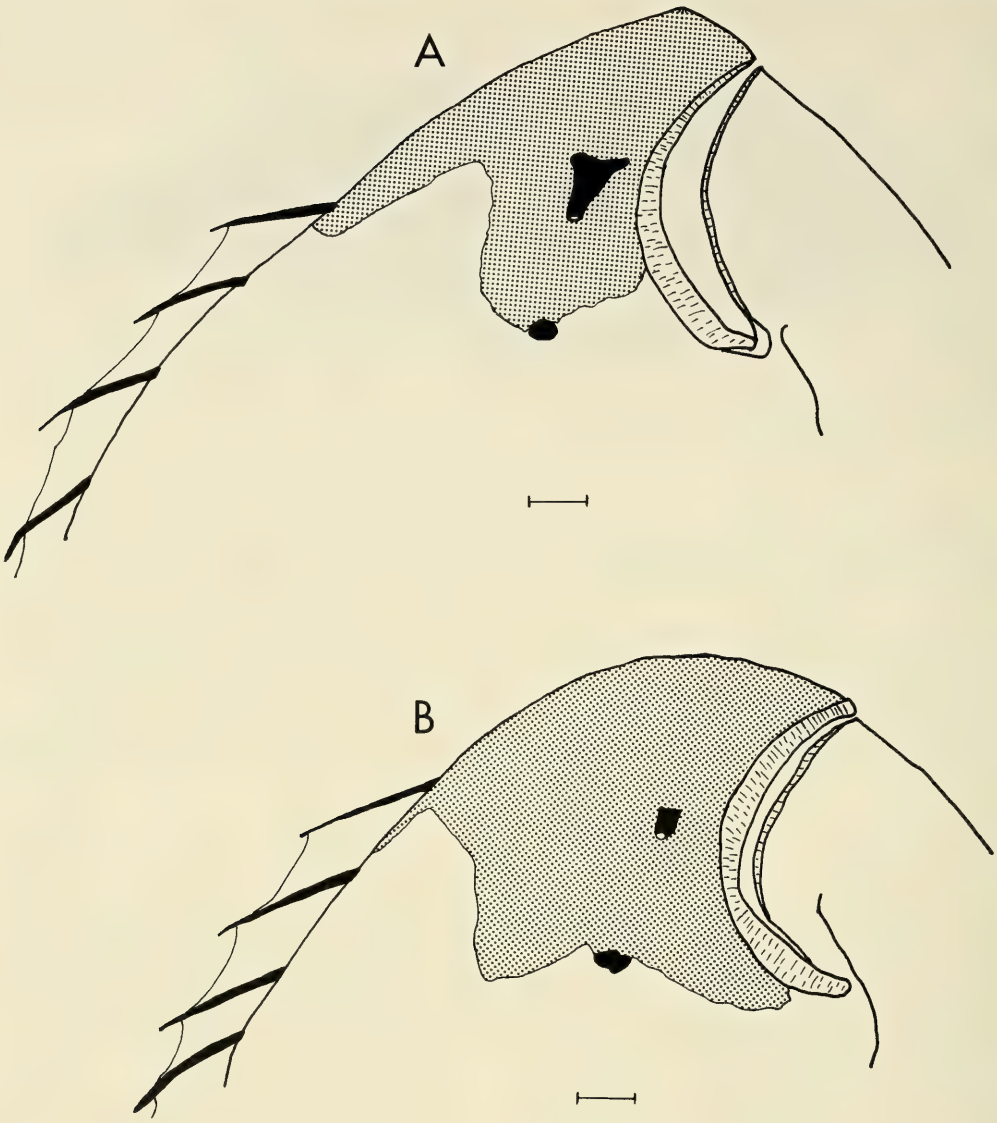


Fig. 2. Lateral view of the blind side of the head highlighting differences in head shape, relative size of the anterior nostril (in black), and relative position of the first dorsal-fin ray (in black) between two eastern Pacific species of *Symphurus*. A) *S. prolatinaris* (USNM 308408). B) *S. melanurus* (UCLA W53-289). Scale bar equals one millimeter.

May 1965. SIO 60–87 (2, 82.1-144.6), approximately off Río San Pedro mouth, 21°46.4′N, 105°25.2′W to 21°50.5′N, 105°44.9′W, 18 m, 8–9 Mar 1960. UA 67-71-9 (2, 110.0–134.0), Sinaloa, Golfo de California, Mazatlan harbor, 20 Sep 1967. SIO 63-517 (122.1), Golfo de Tehuantepec, 14°45′N, 92°35′W, 19 m, 11 Jul 1963. Guatemala.—LACM 20406 (103.8), off San Jose light, 23 Mar 1939. El Salvador.—USNM 308409 (5, 123.6–136.7), Saite, 26 m, 28 Oct 1975. SIO 73-276 (119.8), ca. SW of Punta Amapala (west point of Golfo de Fonseca), 13°5.1–6.5′N, 87°57.6–59.5′W, 27

Fig. 3. Geographic distribution of *Symphurus prolatinaris* based on available study material. Dots may represent more than one collection locality and more than a single specimen from each locality.

m, 17 Apr 1973. Costa Rica.—UCR 1286-10 (116.1), Golfo de Nicoya, in front of Puntarenas Hospital, 16 m, 25 Jul 1979. Ecuador.—CAS 24942 (6, 109.5–125.6), 3°39′00″S, 80°41′00″W, 13 m, 10 Sep 1966. Peru.—CAS 24925 (139.3), 4°51′00″S, 81°20′00″W, 34 m, 2 Jun 1966. CAS 24944 (115.4), 4°48′00″S, 81°17′00″W, 27 m, 2 Jun 1966. IMARPE 67-2337 (161.0), Playa Tortugas, Chimbote, 9 Nov 1967.

Counts but not morphometric information were also taken from the following 112 paratypes (37.8–144.7 mm): Mexico.—SIO 64-877 (4, 50.4–59.8), Baja California Sur, 2 mi SW of Isla Santa Margarita SW of Cerro Santa Margarita on SE end, 24°19.6–19.8′N, 111°46.4–47.1′W, 52 m, 13 Nov 1964. SIO 62-707 (51.5), Baja California Sur, 12½ mi NW of Marquis Pt., 24°05.1′N, 111°02.0′W to 24°06.1′N, 111°03.1′W, 19 m, 4 Dec 1962. UCLA W62-45 (4, 106.2–124.0), Sinaloa, Golfo de California, N of Mazatlan, 27 Feb 1962. UCLA W58-3 (86.3), Nayarit, 1–3 mi N of Ensenada Chi-

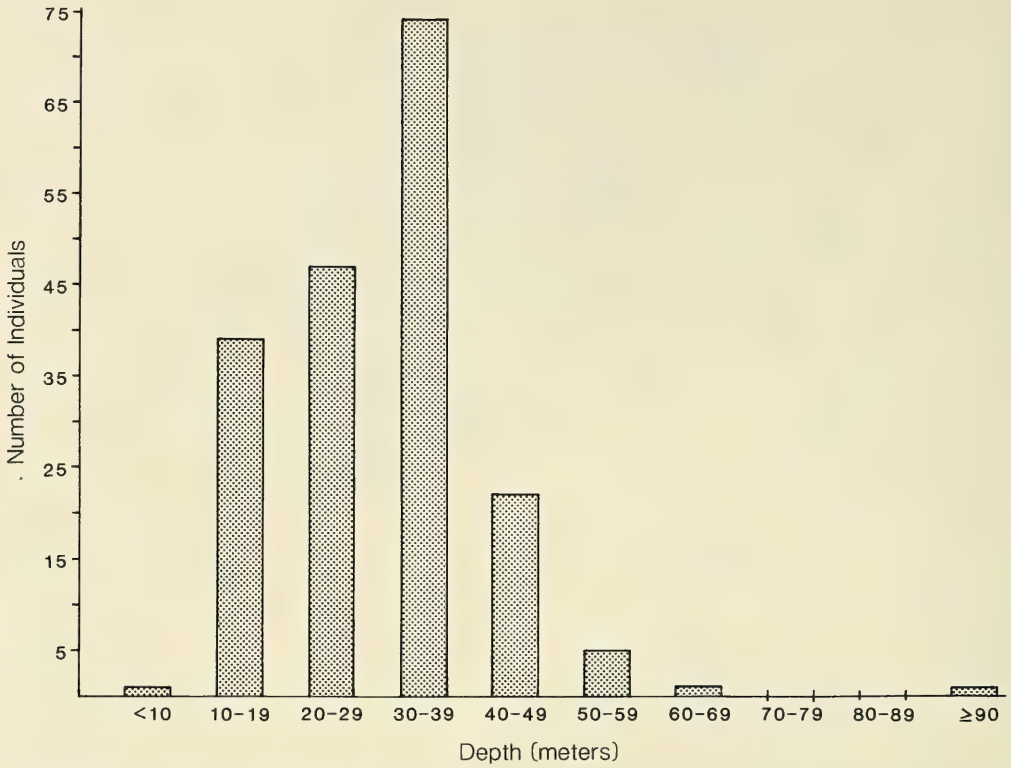


Fig. 4. Frequency histogram of bathymetric occurrence of *Symphurus prolatinaris*. Data are based on numbers of individuals taken at each depth interval.

cala, 22 Jan 1958. SIO 62-70 (83.9), off Nayarit, 22°00.5′N, 105°44.8′W, 29 m, 24 Aug 1961. SIO 62-50 (68.0), Banderas Bay, 20°45.2′N, 105°22.6′W to 20°43.0′N, 105°21.8′W, 24 m, 21 Aug 1961. SIO 65-160 (2, 57.0–72.0), Banderas Bay, 20°44′N, 105°24.6′W, 30 m, 2 Jun 1965. SIO 65-167 (28, 79.1–132.7), Golfo de Tehuantepec, 16°07′N, 95°07′W, 19 m, 7 Jun 1965. SIO 63-501 (12, 73.9–132.8), Oaxaca, Golfo de Tehuantepec, 16°06′N, 95°08′W, 28 m, 8 Jul 1963. SIO 63-502 (8, 62.5–138.6), Golfo de Tehuantepec, 16°02.5′N, 95°07.5′W, 34 m, 8 Jul 1963. SIO 63-503 (3, 83.3–91.6), Oaxaca, Golfo de Tehuantepec, off Salina Cruz, 16°02.5′N, 95°02.5′W, 37 m, 8 Jul 1963. SIO 79-10 (10, 68.5–89.5), off Salina Cruz, Oaxaca, 15°58.5′N, 95°0.76′W to 16°00′N, 95°09.3′W, 41 m, 6 Apr 1978. SIO 63-504 (92.8), Golfo de Tehuantepec, Oaxaca, off Salina Cruz, 15°57.5′N, 95°00′W, 62 m, 8 Jul 1963. SIO 63-507 (79.7), Golfo de Tehuantepec, Oaxaca, off Salina Cruz, 15°50′N, 95°07.5′W, 162 m, 9 Jul 1963. SIO 63-521 (66.2), Golfo de Tehuantepec, 15°41′N, 96°07.5′W, 56 m, 14 Jul 1963. Costa Rica.—LACM 42893-3 (90.6), near Pta. Coyote, 9°44′60″–9°43′42″N, 85°17′42″–85°17′18″W, 31 m, 13 May 1973. SIO 73-297 (73.0), west coast, immediately east of Pta. Judas at east side of entrance of Golfo de Nicoya, 9°27.5′–28.3′N, 84°21.7–24.2′W, 26 m, 22 Apr 1973. SIO 73-298 (30, 37.8–144.7), west coast, SSW off Pta. Judas, eastern point of entrance to Golfo de Nicoya, 9°27.5′N, 84°30.7′W, 31 m, 22 Apr 1973. Peru.—IMARPE 66-2146 (123.0), 5°00′30″S, 81°24.5′W, 3 Jun 1966. UCLA W59-63 (102.2), anchorage at inner harbor, Salaverry (ca. 8°14′S, 79°00′W), 3 Nov 1958.

Diagnosis.—A medium-sized tonguefish, attaining maximum lengths of 161 mm, with

Table 1.—Summary of selected meristic features examined in specimens of *Symphurus prolatinaris*. (Asterisks indicate values for holotype.)

	Dorsal-fin rays											
	102	103	104	105*	106	107	108	109	110	111	112	$\bar{X}$
Frequency	1	3	9	34	28	17	13	2	1	—	1	106.0

	Anal-fin rays									
	85	86	87	88*	89	90	91	92	93	$\bar{X}$
Frequency	1	2	15	34	32	19	4	1	2	88.7

	Caudal-fin rays				
	10	11	12*	13	$\bar{X}$
Frequency	2	3	93	4	12.0

	Total vertebrae					
	54	55	56*	57	58	$\bar{X}$
Frequency	6	47	50	4	2	55.5

	Longitudinal scale rows													
	88	89	90	91	92*	93	94	95	96	97	98	99	100	$\bar{X}$
Frequency	4	4	8	10	15	11	18	5	1	7	3	2	3	93.1

	Transverse scale count									
	37	38*	39	40	41	42	43	44	45	$\bar{X}$
Frequency	2	7	10	19	22	10	5	5	1	40.6

	Head scale rows					
	19	20	21	22	23	$\bar{X}$
Frequency	1	32	46	21	5	21.0

	Pattern	Frequency	%
Interdigitation pattern	1-5-3-2-2*	88	80.7
	1-6-3-2-2	5	4.6
	1-5-4-2-2	4	3.7
	1-4-3-2-2	3	2.8
	1-5-3-3-2	3	2.8
	1-6-2-2-2	3	2.8
	1-5-2-2-2	2	1.8
	1-4-4-2-2	1	0.9

females maturing at sizes from 98 mm; characterized by a 1-5-3-2-2 ID pattern; 12 caudal-fin rays; 102–112 dorsal-fin rays; 85–93 anal-fin rays; 54–58 total vertebrae; four hypurals; lightly-pigmented, triangular, veil-like pupillary operculum; 3–8 small, ctenoid scales on blind sides of the dorsal- and anal-fin rays; unpigmented peritoneum; pronounced tubular anterior nostril on the blind side (Fig. 2); first dorsal-fin ray anterior to vertical through front margin of upper eye; and ocular-side lower jaw usually without a pronounced fleshy ridge on its posterior portion.

Description.—Frequency distributions of meristic data are given in Table 1. ID pattern typically 1-5-3-2-2 (88/108 specimens), less frequently 1-6-3-2-2, 1-4-3-2-2, 1-5-4-2-2, 1-5-3-3-2, 1-6-2-2-2, 1-5-2-2-2, or 1-4-4-2-2. Caudal-fin rays 12 (93/102),

Table 2.—Summary of morphometrics expressed as thousandths of Standard Length (except SL in mm) for the holotype (USNM 308408) and 24 paratypes of *Symphurus prolatinaris*. (Abbreviations defined in text.)

Character	Holotype	Paratypes		
		Range	Mean	*SD*
SL	112.8	103.8–161.0	124.0	12.94
BD	302	259–300	284.0	10.28
PDL	42	21–41	28.2	5.23
PAL	211	165–244	217.5	17.39
DBL	958	959–979	971.4	5.33
ABL	805	745–827	787.1	18.34
PL	78	45–70	58.8	7.04
CFL	99	73–101	91.8	6.37
HL	193	154–214	192.7	12.15
HW	232	208–269	237.0	13.84
POL	128	92–144	127.1	12.01
SNL	43	31–46	38.2	3.88
UJL	47	37–55	44.4	4.21
ED	20	15–21	18.0	1.67
CD	56	40–61	46.7	5.39
UHL	146	118–154	138.1	9.94
LHL	111	94–133	112.3	8.80

rarely 10, 11, or 13. Dorsal-fin rays 102–112, usually 104–108, $\bar{X}$ = 106.0. Anal-fin rays 85–93, usually 87–90, $\bar{X}$ = 88.7. Pelvic-fin rays 4. Total vertebrae 54–58, usually 55–56, occasionally 54 or 57, rarely 58, $\bar{X}$ = 55.5; abdominal vertebrae 9 (3+6). Hypurals 4 (109/109). Longitudinal scale rows 88–100, usually 90–97, $\bar{X}$ = 93.1. Scale rows on head posterior to lower orbit 19–23, usually 20–22, $\bar{X}$ = 21.0. Transverse scales 37–45, usually 39–42, $\bar{X}$ = 40.6.

Summaries of morphometric data are provided in Tables 2–3. Body relatively deep (259–302 SL, $\bar{X}$ = 284); greatest depth in anterior one-third to one-half of body; body tapering fairly rapidly posterior to midpoint. Preanal length 165–244 SL, $\bar{X}$ = 218; shorter than body depth. Head relatively wide (208–269 SL, $\bar{X}$ = 237); somewhat less than body depth. Head length (154–214 SL, $\bar{X}$ = 193); shorter than head width (HW/HL 1.08–1.35, $\bar{X}$ = 1.24). Postorbital length 92–144 SL, $\bar{X}$ = 127. Lower head lobe (94–133 SL, $\bar{X}$ = 112) nearly equal to postorbital length; slightly smaller than upper head lobe (118–154 SL, $\bar{X}$ = 138). Snout relatively short, 159–242 HL, $\bar{X}$ = 199; covered with small ctenoid scales. Dermal papillae well developed on blind side of snout. Anterior nostril on ocular side relatively short; when extended posteriorly usually falling just short of vertical through anterior margin of lower eye. Anterior nostril on blind side conspicuously long and tubular; usually readily distinguishable from dermal papillae on blind side of snout (Fig. 2). Mouth relatively large, 189–266 HL, $\bar{X}$ = 230; posterior margin of maxilla usually reaching vertical through posterior margin of pupil, or posterior margin of lower eye. Chin depth 205–294 HL, $\bar{X}$ = 243; slightly greater than snout length. Lower eye relatively small, 80–105 HL, $\bar{X}$ = 94; eyes usually slightly sub-equal in position with upper slightly in advance of lower eye. Anterior and medial surfaces of eyes partially covered with 3–4 rows of small ctenoid scales; 3–5 small ctenoid scales in narrow interorbital region. Pupillary operculum not well developed, only faintly pigmented, usually triangular and veil-like in appearance (not readily visible in small specimens or those preserved for long periods). Length of dorsal-fin base 958–979 SL, $\bar{X}$ = 971. Dorsal-fin origin far forward, with first dorsal-fin ray anterior to vertical through anterior margin of upper eye; pre-

Table 3.—Summary of morphometrics expressed as thousandths of Head Length (except HW/HL) for the holotype (USNM 308408) and 24 paratypes of *Symphurus prolatinaris*. (Abbreviations defined in text.)

Character	Holotype	Paratypes		
		Range	Mean	*SD*
HW/HL	1.20	1.08–1.35	1.24	0.12
POL	661	477–707	660.1	46.31
SNL	225	159–242	199.0	20.86
UJL	243	189–266	230.2	17.55
ED	101	80–105	94.1	7.78
CD	289	205–294	242.9	27.42
UHL	757	604–891	719.5	63.29
LHL	573	534–689	583.5	38.98
PDL	216	108–210	146.5	27.06

dorsal length relatively short, 21–42 SL, $\bar{X}$ = 28. Length of anal-fin base 745–827 SL, $\bar{X}$ = 787. Blind sides of dorsal and anal fins with 3–8 small, ctenoid scales extending to about mid-point of fin rays. Pelvic fin relatively short, 45–78 SL, $\bar{X}$ = 59; longest pelvic-fin ray, when extended posteriorly, usually reaching first anal-fin ray. Caudal fin relatively short, 73–101 SL, $\bar{X}$ = 92.

Teeth well developed on blind-side dentary and premaxilla. Teeth on ocular-side premaxilla poorly developed, slender, in single row, usually covering only anteriormost one-fifth of bone. Teeth on ocular-side dentary usually absent, occasionally with few teeth present on anterior one-fourth of bone.

Pigmentation.—Light to dark brown background coloration with occasional crossbanding. Crossbands short, nearly always incomplete and offset, not continued onto dorsal- and anal-fin rays. Crossbands on body 5–15 in number; narrow, usually only 3–8 scale rows wide; beginning immediately posterior to opercular opening and continuing to base of caudal fin. Head occasionally with two crossbands about 4–6 scale rows wide; anterior crossband immediately posterior to eyes; posterior band crossing distal margin of operculum. Outer surface of ocular-side operculum usually with same background coloration as body; occasional specimens with dusky blotch on ocular-side opercle resulting from dark pigment of inner opercular lining showing through to outside. Inner linings of both opercles pigmented; that of ocular side always more heavily pigmented; most specimens usually with pigment only on ventral half of inner opercular lining on blind side of body. Isthmus heavily spotted on both sides of body. Ocular-side upper lip usually with heavier concentration of melanophores than lower lip; occasional specimens with dark pigment band on upper lip. Blind side uniformly off-white to yellowish. Peritoneum unpigmented.

Dorsal and anal fins without obvious blotches or spots, but becoming increasingly darker on posterior one-third to posterior one-half of body. Membrane between fin rays usually lighter than membrane covering fin rays, thereby clearly outlining each fin ray. Caudal-fin rays and membrane uniformly darkly pigmented; middle caudal-fin rays occasionally whitish at tip.

Size and sexual maturity.—Of 97 females, 77, ranging from 65.8 to 161.0 mm, are mature with elongate, ripening, or gravid ovaries. The smallest gravid females measure 96.8, 101. 0, and 102.2 mm. Twenty females (50.4–75.6 mm) are immature with ovaries in some phase of elongation. In four of the smallest females (53.5–57.6 mm), ovaries have just begun to elongate, while in 16 others (50.4–75.6 mm), ovaries are only slightly elongate. Males (N = 99) are only slightly smaller (50.8–144.7 mm) than females (50.4–161.0 mm). Sex was not determined for three individuals ranging from 37.8 to 42.9 mm.

Etymology.—The name *prolatinaris* is from the Latin *prolatus* (= elongated) and *naris* (= nostril), in reference to the elongate, blind-side anterior nostril characteristic of this species. The specific epithet is treated as a noun in apposition.

Geographic and bathymetric distribution.—*Symphurus prolatinaris* occurs throughout the tropical and warm temperate coastal waters of the eastern Pacific (Fig. 3), from the southwestern coast of Baja California Sur (24°19.6–19.8′N, 111°46.4–47.1′W) to central Peru (ca. 9°S, 78.5°W). We did not find any specimens of this species among tonguefishes we examined that were collected from within the Gulf of California. The majority of specimens of *S. prolatinaris* were collected from coastal waters of Mexico and Central America. The two northernmost collections, off Baja California Sur, contained only five specimens. Six of seven lots collected south of 5°N latitude contained only solitary individuals, while the seventh collection from this region comprised six specimens. Disjunctions in the distribution indicated in Fig. 3 are pre-

sumed to be an artifact of different collecting intensities, and at this time there is no a priori reason to assume that *S. prolatinaris* does not occur in those regions.

Symphurus prolatinaris has been collected on the inner continental shelf at depths ranging from 9 to 162 m (USNM 308408 and SIO 63-507, respectively). However, based on frequency of capture and relative abundance (Fig. 4), the bathymetric center of occurrence for this species is between 13 and 42 m, where 96% (189 of 197) of the specimens were captured. Only eight specimens, one each captured at the extremes of the depth range (9 m and 162 m, respectively) and six specimens taken between 52–62 m, were collected beyond the 13–42 m depth range.

Geographical variation.—Compared with some other eastern Pacific tonguefishes (Mahadeva 1956, Mahadeva & Munroe 1990), little geographic variation was noted in the numbers of dorsal- and anal-fin rays and total vertebrae for the specimens examined.

Co-occurring Symphurus species.—*Symphurus prolatinaris* has been collected with several other species of *Symphurus,* including *S. melanurus* Clark, *S. chabanaudi, S. callopterus* Munroe & Mahadeva, *S. williamsi* Jordan & Culver, and *S. melasmatotheca* Munroe & Nizinski.

Comparisons.—*Symphurus prolatinaris* is one of eight species of *Symphurus* characterized by a 1-5-3-2-2 ID pattern. All *Symphurus* species with this dorsal pterygiophore arrangement co-occur in shallow, warm-temperate and tropical waters of the eastern Pacific. Among these eight species, *S. prolatinaris* is distinguished in having the combination of high dorsal- and anal-fin ray and total vertebral counts, and a pupillary operculum. Ranges for dorsal- and anal-fin ray counts in *S. prolatinaris* scarcely overlap those for *S. atricaudus, S. melasmatotheca,* and *S. williamsi,* and there is no overlap in total vertebrae counts between these species. *Symphurus prolatinaris* has 102–112 dorsal-fin rays (versus 102 or fewer in these other three species); 85–93 anal-fin rays (versus 85 or less); and 54–58 total vertebrae (versus 53 or less). *Symphurus prolatinaris* differs further from *S. melasmatotheca* in having 12 caudal-fin rays (versus 11 in *S. melasmatotheca*), an unpigmented peritoneum (versus black), 3–8 small ctenoid scales on blind sides of the dorsal- and anal-fin rays (versus scales absent), a lightly-pigmented, veil-like pupillary operculum (versus darkly pigmented, well-developed pupillary operculum), and the first dorsal-fin ray anterior to the vertical through the front margin of the upper eye (versus first dorsal-fin ray at a point between the verticals through the mid-eye and posterior margin of the upper eye in *S. melasmatotheca*).

There is some overlap between the dorsal- and anal-fin ray and total vertebrae counts of *S. prolatinaris* and *S. melanurus.* However, counts for *S. prolatinaris* range higher (dorsal-fin rays 102–112 versus 95–103 in *S. melanurus*; anal-fin rays 85–93 versus 78–87; and 54–58 total vertebrae versus 50–54). Despite overlap in some meristic features, these species differ in many other anatomical features, including the size of the blind-side anterior nostril, which in *S. prolatinaris* is pronounced, elongate, and tubular, and is distinctly visible from the dermal papillae covering the blind-side snout. The blind-side anterior nostril of *S. melanurus,* in contrast, is a short, rounded, nub-like structure that is never as distinct as that of *S. prolatinaris* and frequently is hardly distinguishable from the dermal papillae on the blind-side snout (see Fig. 2). *Symphurus prolatinaris* also lacks the well-developed fleshy ridge on the posterior portion of the ocular-side lower jaw that is evident in *S. melanurus.* Furthermore, in *S. prolatinaris,* the blind sides of the dorsal- and anal-fin rays have about 3–8 small, ctenoid scales extending to about the midpoint of the fin rays, while in *S. melanurus* there are either no scales present, or at most, the blind sides of the dorsal- and anal-fin

rays have 1–2 small ctenoid scales present only along basal portions of fin rays.

Dorsal- and anal-fin ray, and vertebral counts of *S. prolatinaris* overlap extensively those of the three remaining eastern Pacific tonguefishes characterized by a 1-5-3-2-2 ID pattern (*S. undecimplerus* Munroe & Nizinski, *S. elongatus* (Günther), and *S. chabanaudi*). *Symphurus prolatinaris* differs from *S. undecimplerus* primarily in caudal-fin ray counts (12 versus 11 in *S. undecimplerus*), presence of scales on the blind sides of the dorsal- and anal-fin rays (versus their absence), by its smaller eye (80–105 HL versus 104–153 HL), and in its modally higher counts for dorsal-fin rays (102–112 versus 97–105), anal-fin rays (85–93 versus 80–87), and total vertebrae (54–58 versus 52–56).

Fin-ray and vertebral counts of *S. prolatinaris* completely overlap those of *S. elongatus* and *S. chabanaudi.* However, the new species is distinct from these other species. *Symphurus prolatinaris* differs from *S. elongatus* primarily in having a pupillary operculum and small ctenoid scales on the blind sides of the dorsal- and anal-fin rays (both characters absent in *S. elongatus*), a larger eye (15–21 SL versus 9–15 SL in *S. elongatus*), and a larger anterior nostril on the blind side relative to that of *S. elongatus. Symphurus prolatinaris* differs most notably from *S. chabanaudi* in possessing a pupillary operculum (absent in *S. chabanaudi*) and in lacking a large, dark-brown or black blotch on the outer surface of the ocular-side opercle (present in *S. chabanaudi*). Also, the dorsal-fin origin is more anterior in *S. prolatinaris,* with the first dorsal-fin ray anterior to the vertical through the front margin of the upper eye, while in *S. chabanaudi* the first dorsal-fin ray is usually only at or between verticals through the front margin and mid-point of the upper eye.

Some meristic features of *S. prolatinaris* are similar also to those of other eastern Pacific tonguefishes, including *S. callopterus, S. leei* Jordan & Bollman, *S. diabolicus* Mahadeva & Munroe, and *S. microlepis* Garman, although it is possible to readily distinguish *S. prolatinaris* from any of these species. *Symphurus prolatinaris* differs from all four species in having a 1-5-3-2-2 ID pattern (versus 1-3-4-2-2 in *S. callopterus,* 1-4-3-2-2 in *S. leei,* and 1-3-2-2-2 in *S. diabolicus* and *S. microlepis*). *Symphurus prolatinaris* also differs from *S. diabolicus* and *S. microlepis* in having 4 hypurals, a pupillary operculum, and an unpigmented peritoneum (versus 5 hypurals, no pupillary operculum, and a black or spotted peritoneum). *Symphurus prolatinaris* differs further from *S. callopterus* in having uniformly pigmented dorsal and anal fins (versus dorsal and anal fins with a series of alternating pigmented blotches and unpigmented areas), and in the small ctenoid scales on the blind sides of the dorsal- and anal-fin rays (absent in *S. callopterus*). In addition to lacking scales on the blind sides of the dorsal and anal fins, *S. leei* also differs from *S. prolatinaris* in having the head length greater than its width, while in *S. prolatinaris* head length is noticeably shorter than head width.

The combination of a 1-5-3-2-2 ID pattern, 12 caudal-fin rays, pupillary operculum, small scales on the blind sides of the dorsal- and anal-fin rays, and unpigmented peritoneum distinguishes *S. prolatinaris* from all other species of *Symphurus* occurring in Atlantic or Indo-Pacific waters.

Additional Material of *S. prolatinaris* Examined

Non-type material examined but not counted or used for morphometric information (64 specimens; 37.8–144.7 mm): Mexico.—SIO 79-11 (12, 54.2–77.8), Salina Cruz, Oaxaca, 16°00′N, 95°09.9′W, 42 m, 6 Apr 1978. SIO 73-257 (22, 42.9–126.7), off NE shore of Golfo de Tehuantepec, 15°30.0–31.0′N, 93°22.0–23.1′W, 23 m, 10 Apr 1973. Costa Rica: SIO 73-298 (30, 37.8–144.7), west coast, SSW off Punta Judas,

eastern point of entrance to Golfo de Nicoya, 9°27.5′N, 84°30.7′W, 31 m, 22 Apr 1973.

Acknowledgments

We thank R. Gibbons who assisted with photography. The following curators and support staff generously provided space and arranged for loan of specimens: W. Eschmeyer and D. Catania (CAS); E. Anderson (formerly CAS, now at J. L. B. Smith Institute of Ichthyology); N. Chirichigno and J. Vélez (IMARPE); R. Lavenberg, J. Seigel, R. Feeney (LACM); R. Rosenblatt, D. Gibbons, H. J. Walker (SIO); L. Knapp (Smithsonian Oceanographic Sorting Center); F. Zapata and M. Brogan (UA); D. Buth (UCLA); W. Bussing (UCR); and J. Clayton and J. Howe (USNM). An earlier draft of the manuscript benefitted from critical reviews provided by B. Collette, D. Hensley, R. Vari, and J. Williams. Portions of this study were initiated while the first author was a Smithsonian postdoctoral fellow in the Division of Fishes at the National Museum of Natural History.

Literature Cited

Chirichigno F., N. 1974. Clave para identificar los peces marinos del Perú.—Informes Instituto del Mar del Perú 44:1–387.

Hildebrand, S. F. 1946. A descriptive catalog of the shore fishes of Peru.—Bulletin of the United States National Museum 189:1–530.

Mahadeva, N. 1956. A review of the tonguefishes of the eastern Pacific, with descriptions of six new species. Unpublished Ph.D. dissertation, University of California at Los Angeles, 272 pp.

———, & T. A. Munroe. 1990. Three new species of symphurine tonguefishes from tropical and warm temperate waters of the eastern Pacific (*Symphurus*: Cynoglossidae: Pleuronectiformes).—Proceedings of the Biological Society of Washington 103:931–954.

Meek, S. E., & S. F. Hildebrand. 1928. The marine fishes of Panama.—Field Museum of Natural History, Publication 249, Zoological Series Volume 15 (Part 3):709–1045.

Munroe, T. A. 1990. Eastern Atlantic tonguefishes (*Symphurus*: Cynoglossidae, Pleuronectiformes), with descriptions of two new species.—Bulletin of Marine Science 47:464–515.

———, & M. N. Mahadeva. 1989. *Symphurus callopterus* (Cynoglossidae, Pleuronectiformes), a new deepwater tonguefish from the eastern Pacific.—Proceedings of the Biological Society of Washington 102:458–467.

———, & M. S. Nizinski. 1990. *Symphurus melasmatotheca* and *S. undecimplerus* (Cynoglossidae, Pleuronectiformes), two new eastern Pacific tonguefishes with eleven caudal-fin rays.—Copeia 1990:985–996.

(TAM, MSN) National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, D.C. 20560; (MNM) Department of Biology, University of Wisconsin–Oshkosh, Oshkosh, Wisconsin 54901. (All correspondence should be addressed to the first author.)

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 459–467

THREE NEW SPECIES OF THE BENTHO-PELAGIC FISH GENUS *PLAGIOGENEION* FROM THE SOUTHERN PACIFIC AND INDIAN OCEANS (TELEOSTEI: EMMELICHTHYIDAE)

N. V. Parin

Abstract.—*Plagiogeneion geminatum,* described from eight specimens from a seamount on the Nazca submarine ridge in the southeastern Pacific at 200 m, is most similar to *P. rubiginosum,* but differs in having more transverse scales (37–39 vs. 29–34), and a slightly shorter pectoral fin and upper jaw. *Plagiogeneion unispina,* described from five specimens from a seamount of the Sala y Gomez submarine ridge at 280–310 m, and *P. fiolenti,* described from 35 specimens from Walters Shoals in the southwestern Indian Ocean at 180–300 m, are distinct from other congeners in having only the lower opercular spine sharp and a more slender body. The former has more lateral line and transverse scales than *P. fiolenti* (67–73 vs. 60–70; 29–31 vs. 31–33).

According to the revision of the Emmelichthyidae by Heemstra & Randall (1977), the genus *Plagiogeneion* Forbes includes two species, *P. rubiginosum* (Hutton) known from New Zealand (type locality), southeastern Australia, St. Paul and Amsterdam Islands, South Africa and Vema Seamount, and *P. macrolepis* McCulloch with very restricted distribution in the Great Australian Bight. These two species are easily recognized by the number of lateral-line scales (67–74 in *P. rubiginosum* vs. 48–51 in *P. macrolepis*). According to Eschmeyer (1990: 317), the generic name *Plagiogeneion* is neuter so the ending of the adjectival species name *rubiginosus* must be modified to *rubiginosum.*

When taking part in an expedition to the southeast Pacific in 1984, I collected five emmelichthyids that were identified, using the key in Heemstra & Randall (1977), as *P. rubiginosum.* In 1986 I. I. Konovalenko, a fishery biologist with the AtlantNIRO Fisheries Institute (Kaliningrad, USSR), obtained from the same general area another eight specimens also referable to *P. rubiginosum* using Heemstra and Randall's key, but evidently different from the specimens in the first collection. When comparing this material with other available specimens of *Plagiogeneion,* I found that three specimens from Walters Shoals, a seamount in the southwestern Indian Ocean also did not fit all characters of *P. rubiginosum.* In 1988, numerous additional specimens of the West Indian Ocean species were collected at Walters Shoals during the R/V *Vityaz* expedition (Collette & Parin 1991). Having very limited material of *Plaigiogeneion* from other than the localities mentioned, I have decided not to try to revise the genus at this time but to simply describe the three apparently new species.

Materials and methods.—Material of the three new species is listed in the species accounts. For comparisons, data on 31 specimens of *P. rubiginosum* received from P. Heemstra were used (counts and measurements of 18 specimens, 91–442 mm SL from New Zealand and New South Wales, 7 specimens, 235–350 mm from off South Africa, and 6 specimens, 120–189 mm from St. Paul and Amsterdam Is.). Additional material examined by me include a *P. rubiginosum*

(246 mm SL) from the Tasman Sea (37°42′S, 167°40′E; ZIN 49828), 1 (178 mm) from South Africa (37°42′S, 17°23′E; ZIN 48829) and 1 (108 mm) from Walters Shoals (33°05′S, 43° 42′E; ZIN 49830) and 1 specimen of *P. macrolepis* (198 mm; 33°16′S, 129°04′E; ZIN 38591). Not being convinced that the "*P. rubiginosum*" from New Zealand–Australia, St. Paul–Amsterdam and South Africa are conspecific (all are deep-bodied but differ in pectoral fin length, number of pectoral rays and scales between dorsal-fin origin and lateral line; see Tables 1, 2), I compare the three new species with each of these allopatric populations.

Measurements and counts were made as indicated in Heemstra & Randall (1977). Number of "scales in oblique transverse row" means the sum of scales between the middle of the spinous dorsal fin and the lateral line plus the lateral line scale plus the scales between the lateral line and anal fin origin. Counts of bilateral elements were made on both sides of the body.

In the species descriptions, characters of the paratypes (when different from the holotype) are given in parentheses. Type specimens are deposited in Zoological Institute, Leningrad (ZIN) (including all holotypes), Australian Museum, Sydney (AMS), Los Angeles County Museum (LACM), National Museum of Natural History, Washington, D.C. (USNM), J.L.B. Smith Institute of Ichthyology, Grahamstown (RUSI) and Zoological Museum of Moscow University (ZMMU). SL denotes standard length; HL, head length.

Plagiogeneion geminatum, new species
Fig. 1a

Types.—Holotype: ZIN 49821, 270 mm SL, male; southeastern Pacific, Nazca Ridge, 22°05′S, 81°14′W; commercial pelagic trawl at 200 m; I. I. Konovalenko; 11 Nov 1985.

Paratypes.—ZIN 49822 (3, 262–280), USNM 316518 (1, 266); RUSI 35612 (1, 250); ZMMU 18276 (2, 253–257)—same data as holotype.

Diagnosis.—Body depth 30–33% SL; body width 16–18.5% SL; pectoral-fin length 27–28% SL, both opercular spines sharp; 37–39 scales in oblique transverse row; 69–74 scales in lateral line; pectoral-fin rays 20–21; upper-jaw length 40–42% HL, maxilla width 16–17.5% HL; teeth present on vomer and palatines.

Description.—Counts and measurements are summarized in Tables 2 and 3.

Body depth 3.3 (3.0–3.3), head length 3.5 (3.4–3.6) times in SL. Body depth/width = 1.7 (1.8–2.0). Scales strongly ctenoid, 11 (11–12) between middle dorsal spines and lateral line and 26 (25–26) between the latter and anal fin origin. Pectoral fin long, almost equal to head length. Bony orbit 3.4 (3.1–3.4) times in head length, eye diameter almost equal to interorbital width. Snout length a little less than interorbital width. Upper jaw length/width = 2.5 (2.3–2.5). Ventral edge of preorbital bone finely serrate. Posterior edge of opercle with two sharp and rather strong spines. Narrow band of small sharp teeth at front of both jaws; vomer and palatines with a few small sharp teeth. Gill rakers 12 + 30 (11–13 + 28–31). Pyloric caeca 9–10. Caudal peduncle depth/width = 1.8 (1.7–2.0). Scales around caudal peduncle 35 (35–37).

Color when fresh unknown.

Comparisons.—Most similar to *P. rubiginosum* populations from the type locality (New Zealand) in body proportions and meristics but differs from this species in smaller and more numerous scales along the dorsal and ventral edges of body; as a result the total number of transverse scales is greater in *P. geminatum* (37–39, $\bar{X}$ 37.75 vs. 29–34, $\bar{X}$ 31.42). Also, pectoral fin and upper jaw are slightly shorter in *P. geminatum* than in *P. rubiginosum* from New Zealand and Australia.

Other species of *Plagiogeneion* (including "*P. rubiginosum*" from South Africa and St. Paul–Amsterdam) have shorter pectoral fins

Table 1.—Selected proportional characters of *Plagiogeneion rubiginosus* from different localities (based on data presented by P. Heemstra and examined specimens).

	New Zealand and Australia	South Africa	St. Paul and Amsterdam Ids.
Standard length, mm	91–442	108–350	120–189
Greatest depth of body, % SL	31.0–35.5	30.8–34.8	30.7–32.3
Pectoral fin length, % SL	28.0–30.6	21.6–27.2	23.5–25.6
Maxillary width, % HL	41.6–46.8	43.3–45.9	40.4–44.5

(less than 27% SL). Also, *P. unispina* and *P. fiolenti* have more elongate bodies (depth 28.5–30% SL), no vomerine or palatine teeth, and only one (lower) opercular spine well developed (in both these the upper one is rounded or indistinct). *Plagiogeneion macrolepis* has many fewer lateral-line scales (48–52).

Etymology.—Named for its close similarity to its geminate congener, *P. rubiginosum.*

Distribution.—Known only from a single seamount of the Nazca submarine ridge in the southeast Pacific at 200 m depth.

Plagiogeneion unispina,
new species
Fig. 1b

Types.—Holotype: ZIN 49823, 239 mm SL, male: 25°58′S, 100°36′W; bottom otter trawl; depth 310–290–300 m; N. V. Parin and Y. P. Pavlov; 5 Oct 1984.

Paratypes.—ZIN 49824 (2, 152–236); USNM 316517 (1, 178); RUSI 35613 (1, 173)—same data as holotype. Paratypes, especially both ZIN specimens, are in poor condition because the trawl was badly damaged and the specimens spent 5 days in twisted scraps of the net before their discovery and preservation.

Diagnosis.—Body depth 28–30% SL; body width 13–15% SL; pectoral-fin length 24–26.5% SL; only lower opercular spine sharp; 67–73 scales in lateral line; 29–31 scales in oblique transverse row; pectoral-fin rays 21–23; upper jaw length 39–40.5% HL, maxilla width 13–15% HL; no teeth on vomer or palatines.

Description.—Counts and measurements are summarized in Tables 2 and 3.

Body depth 3.4 (3.4–3.5, 3.9 in smallest paratype 152 mm SL), head length 3.5 (3.3–3.6) times in SL. Body depth/width = 2.0 (1.9–2.2) . Scales feebly ctenoid, 9 left and 8 right (8–9) between middle dorsal spines and lateral line and 20 (19–21) between the latter and anal fin origin. Pectoral fins shorter than head length. Bony orbit 3.3 (2.8–3.1) times in head length, eye diameter approximately equal to interorbital width. Snout length a little less than interorbital width. Upper-jaw length/width = 2.6 (2.6–2.7). Ventral edge of preorbital bone finely serrate. Posterior edge of opercle with rounded (rounded or obtuse) upper projection and sharp spine below. Narrow band of 2–3 rows of small teeth at front of both jaws; vomerine and palatine teeth absent. Gill rakers 12 + 28 (9–12 + 27–29). Pyloric caeca 11. Caudal peduncle depth/width = 2.4 (2.1–2.4). Scales around caudal peduncle 30 (30–31).

Color of fresh holotype: body and fins uniformly red, tips of caudal fin black.

Comparisons.—Resembles *P. fiolenti* in many characters including unequal development of opercular spines, slender body depth, and short pectoral fins. These species can be distinguished by number of lateral-line scales (67–73, $\bar{X}$ 69.6 in *P. unispina* vs. 60–70, $\bar{X}$ 66.0 in *P. fiolenti*), and transverse scales (29–31 vs. 31–33), by maxilla width (13–15 vs. 14.5–16.5% HL) and indices of

Table 2.—Meristics of *Plagiogeneion rubiginosus, P. geminatus, P. unispina* and *P. fiolenti.*

	Fin rays													
	Pectoral					Dorsal					Anal			
	19	20	21	22	23	XII	XIII	10	11	12	III	9	10	11
P. rubiginosus														
Australia–New Zealand	—	16	17	1	—	18	1	3	15	1	19	—	19	—
South Africa	6	8	2	—	—	9	—	1	8	—	9	—	8	1
St. Paul–Amsterdam	—	—	5	6	—	6	—	—	6	—	6	—	6	—
P. geminatus	—	11	5*	—	—	8*	—	—	8*	—	8*	—	8*	—
P. unispina	—	—	1	8*	1	5*	—	—	5*	—	5*	—	5*	—
P. fiolenti	—	23*	40*	7	—	34*	1	4	31*	—	35*	2	32*	1

	Lateral line scales														
	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
P. rubiginosus															
Australia–New Zealand	—	—	—	—	—	—	—	1	2	1	9	2	2	1	2
South Africa	—	—	—	—	—	—	1	2	4	—	1	2	1	—	—
St. Paul–Amsterdam	—	—	—	—	—	—	—	1	1	—	—	2	2	—	—
P. geminatus	—	—	—	—	—	—	—	—	—	1	4*	4	4*	2	1
P. unispina	—	—	—	—	—	—	—	2*	—	3*	1	1	2	1	—
P. fiolenti	1	1	1	3*	7*	11	8	8	8	5	1	—	—	—	—

	Scales D/LL						Scales LL/A							
	7	8	9	10	11	12	19	20	21	22	23	24	25	26
P. rubiginosus														
Australia–New Zealand	1	8	9	—	2	—	—	—	3	3	6	1	—	—
South Africa	—	—	1	8	2	2	—	—	—	1	3	3	—	—
St. Paul–Amsterdam	—	3	2	—	—	—	—	—	—	1	—	—	—	—
P. geminatus	—	—	—	—	13*	3	—	—	—	—	—	—	5	11*
P. unispina	—	6	4*	—	—	—	1	8*	1	—	—	—	—	—
P. fiolenti	—	—	9*	57	4	—	—	4	30*	36	—	—	—	—

Table 2.—Continued.

	Fin rays																								
	Pectoral					Dorsal								Anal											
	19	20	21	22	23	XII	XIII	10	11	12	III	9	10	11	Circumpeduncle scales						Gill rakers				
															30	31	32	33	34	35	36	37	38	39	40	41	42	43
P. rubiginosus																												
Australia–New Zealand	—	5	7	4	1	—	—	—	—	3	3	6	6	1	2													
South Africa	—	1	2	1	—	1	—	—	1	1	3	1	—	—	—													
St. Paul–Amsterdam	—	1	2	2	—	—	—	—	1	1	2	—	1	—	—													
P. geminatus	—	—	—	—	—	3*	3	2	—	—	—	1	1	5*	1													
P. unispina	3*	2	—	—	—	—	—	—	—	3	5	2*	—	—	—													
P. fiolenti	8	19*	7	1	—	—	—	—	6	8	15	4	2*	—	—													

For *P. rubiginosus* data of P. Heemstra are included. Characters of the holotypes marked by an asterisk.

body compression (body depth/width 1.9–2.2 vs. 1.6–1.8, peduncle depth/width 2.1–2.4 vs. 1.8–2.0). The apparent differences in body depth may be due to the poor condition of the paratypes.

Other species of the genus differ from *P. unispina* in deeper body, narrower maxilla and opercular spines equally developed. Also, *P. rubiginosum* from New Zealand–Australia and *P. geminatum* have longer pectoral fins (28–30.5 and 27–28% SL).

Etymology.—The name refers to one of the most important diagnostic features of the species (presence of a single sharp spine on opercle).

Distribution.—All specimens were collected in the same trawl taken at a seamount on the western part of the Sala y Gomez submarine ridge at 280–310 m depth.

Plagiogeneion fiolenti, new species
Figs. 1c, 2a

Types.—Holotype: ZIN 49825, 270 mm SL, male; near Walters Shoals; commercial pelagic trawl at about 250 m; A. S. Piotrovsky; 28 Jul 1984 (R/V *Fiolent,* Sta. 44).

Paratypes.—ZIN 49826 (2, 200–205)—same data as holotype. ZIN 49827 (5, 158–206); 33°07′S, 43°51′E; bottom shrimp-trawl at 240–300 m; 24 Dec 1988 (R/V *Vityaz,* Sta. 2767). ZMMU 18277 (14, 127–170); 33°08′S, 43°51′E; bottom shrimp-trawl at 180–300 (700) m; 24 Dec 1988 (R/V *Vityaz,* Sta. 2768). USNM 307758 (2, 160–164), LACM 44784-1 (2, 250–152), and AMS uncat. and RUSI uncat. (9, 131–166)—same data as ZMMU 18277.

Non-types—ZMMU 18278 (8, 112–232); 34°57′S, 81°10′E; commercial pelagic trawl at 230 m; 6 Jul 1988 (R/V *Fiolent,* no sta. number).

Diagnosis.—Body depth 28–30% SL; body width 16–19.5% SL pectoral fin 24–26.5% SL; only lower opercle spine sharp; 60–70 (usually 64–68) scales in lateral line; 31–33 scales in oblique transverse row; pectoral-

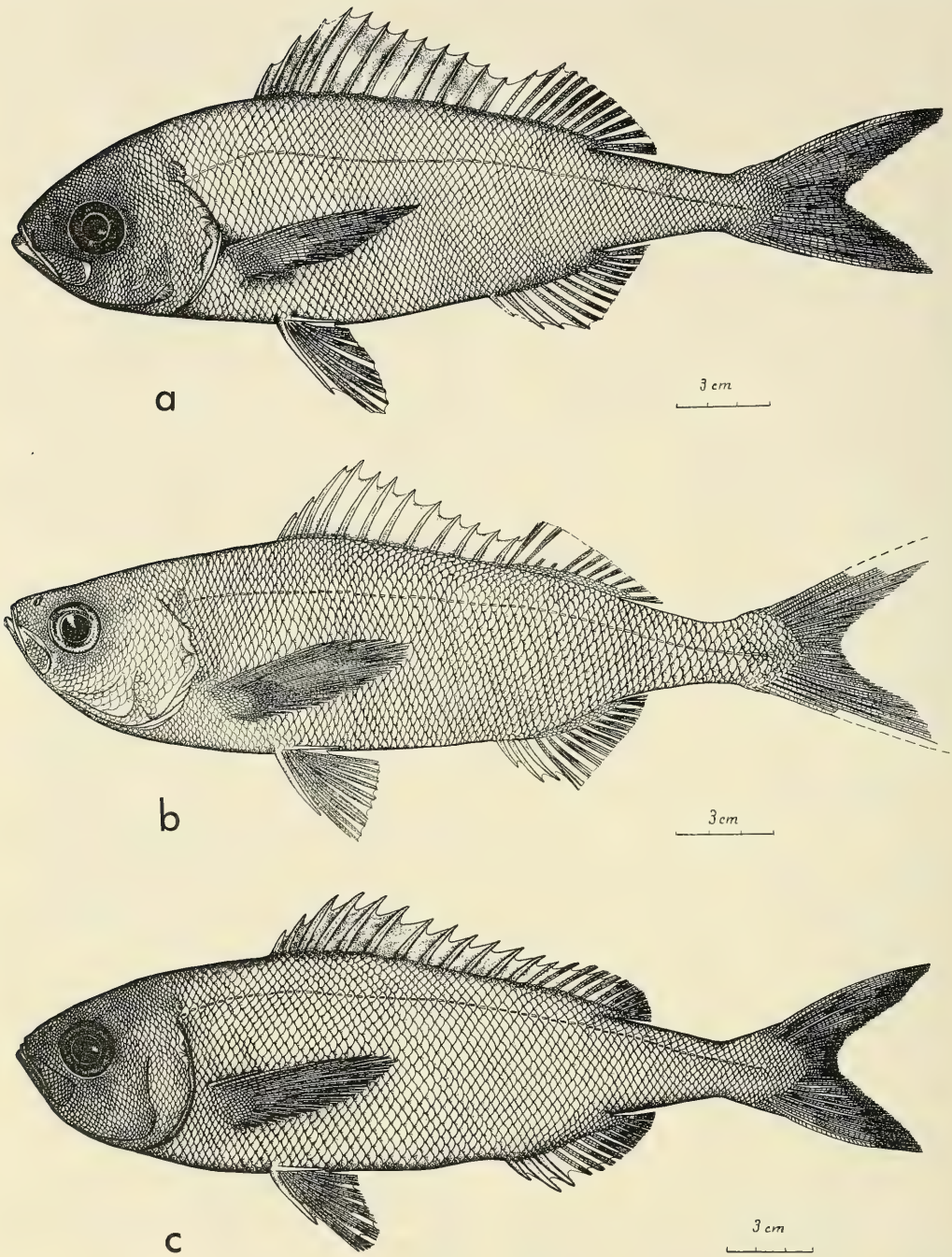


Fig. 1a. *Plagiogeneion geminatum* sp. n., holotype, ZIN 49821, 270 mm SL. b. *Plagiogeneion unispina* sp. n., holotype, ZIN 49823, 239 mm SL. c. *Plagiogeneion fiolenti* sp. n., holotype, ZIN 49825, 270 mm SL.

Table 3.—Proportional measurements of *Plagiogeneion geminatus, P. unispina* and *P. fiolenti.*

	P. geminatus		*P. unispina*		*P. fiolenti*	
	Holotype	7 paratypes	Holotype	4 paratypes	Holotype	12 paratypes
Standard length, mm	270	251–280	239	152–236	270	149–206
In percentage of SL:						
Greatest body depth	30.8	30.4–33.1	29.2	28.3[1]–29.8	28.9	28.3–30.0
Greatest body width	16.8	16.2–18.5	14.4	13.0–14.9	17.8	16.1–19.5
Head length	28.5	18.4–29.7	28.5	27.6–30.2	27.2	30.3–33.3[2]↓
Eye diameter	7.8	7.9–8.6	7.4	8.1–9.9 ↓	7.9	9.7–13.4 ↓
Orbit diameter	8.5	8.7–9.3	8.5	8.9–10.5↓	9.0	10.9–14.1 ↓
Interorbital width	8.2	7.9–8.4	7.9	8.1–8.7	9.6	8.8–9.5 ↑
Upper jaw length	11.9	11.7–12.2	10.5	10.7–11.8	11.5	11.6–14.1
Upper jaw width	4.7	4.7–5.0	4.0	3.9–4.6	4.6	4.6–5.3
Predorsal distance	37.4	37.4–38.6	37.2	38.8–39.7	36.3	37.6–41.0 ↓
Distance snout to anus	64.0	64.0–66.9	67.5	63.2–65.7	64.4	63.6–67.8
Spinous dorsal fin base	30.8	30.4–32.6	28.7	28.3–31.3	28.3	28.6–30.3
Pectoral fin length	27.8	27.2–28.2	24.1	24.1–26.3	25.6	23.9–26.6
Pelvic fin length	18.2	17.4–19.2	18.0	18.5–20.6	16.1	16.4–18.7 ↓
Anal fin length	22.6	22.0–23.8	22.6	22.0–22.8	20.6	20.5–23.8
Caudal fin length	32.6	30.4–34.4	30.1	27.9–28.7	—	29.0–33.0
Caudal peduncle depth	8.0	7.8–8.4	8.2	7.8–8.2	7.4	7.4–8.0
Caudal peduncle width	4.4	4.0–4.8	3.4	3.3–4.0	3.9	3.7–4.4
Longest dorsal fin spine	15.2	13.5–16.0	12.8	13.4–15.8	10.7	10.9–13.7
Penultimate dorsal spine	7.8	7.1–8.0	7.5	8.4–8.7	6.5	5.7–6.3
Last dorsal fin spine	6.7	7.5–8.5	—	7.5–9.8	6.3	5.1–7.4
First anal fin spine	—	4.9–5.8	5.2	5.1–5.9	4.1	4.4–5.8
Third anal fin spine	9.2	8.5–9.4	—	8.7–9.5	8.3	7.6–9.3
Distance ventral fin to anus	9.9	9.2–11.2	10.9	7.0–10.3	11.9	7.0–11.5 ↑

[1] 25.6 in the paratype 152 mm SL; [2] ↓ and ↑ — proportion decreases or increases with increasing SL.

fin rays 20–22; upper-jaw length 40–42.5% HL, maxilla width 14.5–16.5% HL; no teeth on vomer or palatines.

Description.—Counts and measurements are summarized in Tables 2 and 3.

Body depth 3.5 (3.3–3.5), head length 3.7 (3.0–3.3) times in SL. Body depth/width = 1.6 (1.6–1.8). Scales feebly ctenoid, 9 (8–10) between middle dorsal spines and lateral line and 21 (20–22) between the latter and anal fin origin. Pectoral fins shorter than head length. Bony orbit 3.0 (2.3–2.8) in head length, eye diameter less than interorbital width (equal to interorbital width in two paratypes 200 and 205 mm SL). Snout length less than interorbital width. Upper jaw length/width = 2.5 (2.4–2.8). Ventral edge of preorbital bone finely serrate. Posterior edge of operculum with rounded (rounded or obtuse) upper projection and sharp spine below. Narrow band of small teeth at front of both jaws; vomerine and palatine teeth absent. Gill rakers 13 + 28 (11–13 + 26–28). Pyloric caeca 10–13 in 6 paratypes. Caudal peduncle depth/width 1.6 (1.6–1.8). Scales around caudal peduncle 31 (30–33).

Color of freshly collected *Vityaz* paratypes (color photograph taken immediately after capture is published in Collette & Parin, 1991: pl. Ig): body and head reddish pink dorsally becoming silvery laterally and ventrally; pectoral and caudal fins pink, the latter with blackish tips; other fins almost transparent. Holotype and *Fiolent* paratypes "reddish green" as reported by the collector; in alcohol these are much darker than any other *Plagiogeneion* examined.

Remarks.—Differences between the holotype and paratypes in head length, orbit and eye diameter, and interorbital width

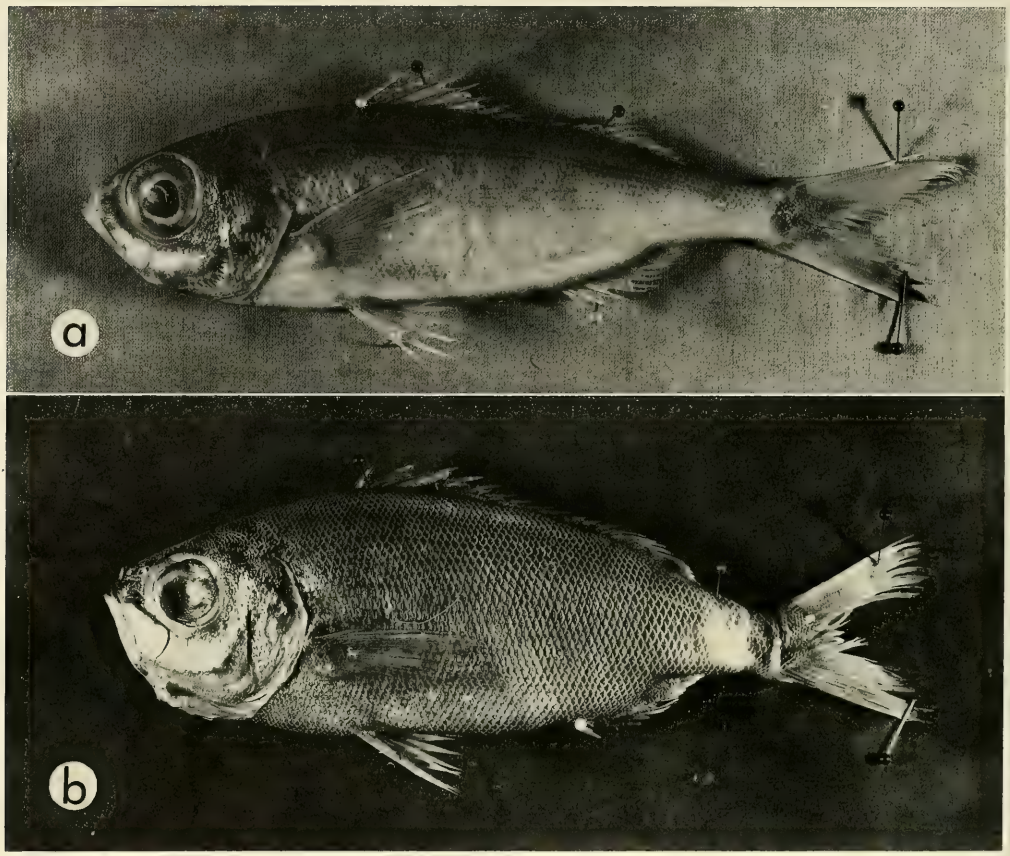


Fig. 2. Similar sized subadult specimens of *Plagiogeneion fiolenti* (185 mm SL, a) and South African *P. rubiginosum* (178 mm SL, b).

(Table 3) are apparently connected with allometric growth.

Non-type specimens collected at an unnamed seamount of the East Indian Ridge do not differ from the type-series in any character and are considered conspecific.

Comparisons.—The characters distinguishing *P. fiolenti* from the most similar species, *P. unispina,* are considered in the latter species account.

Other congeners have a deeper body, two sharp opercular spines, and different ranges of numbers of lateral-line scales (48–51 in *P. macrolepis,* 67–74 in all others).

Distributions of *P. fiolenti* and South African "*P. rubiginosum*" seem to overlap as one specimen 108 mm SL (ZIN 49830) recently collected at Walters Shoals (trawling depth 870–880 m) has all diagnostic characters of the latter (greatest body depth 33.3% SL, pectoral-fin length 21.6% SL, P 20/20, lateral-line scales 68/70, scales between the middle of spinous dorsal fin and lateral line 12). Distinctions between similar sized specimens of the two mentioned forms in general appearance are evident from Fig. 2.

Etymology.—Named for the R/V *Fiolent* from which the holotype and two paratypes were collected in 1984.

Distribution.—Known from the vicinities of Walters Shoals, an isolated submarine seamount in the southwestern Indian Ocean (about 400 miles south of Madagascar), and

from another seamount located at the same latitude but in the eastern Indian Ocean (34°57′S, 81°10′E). It is likely that the record of *P. rubiginosum* from the unnamed seamount east of Walters Shoals (34°54′S, 53°14′E; Duhamel, 1984) also refers to *P. fiolenti.*

Acknowledgments

I thank the collectors of the type material, Ivan I. Konovalenko and Alexei S. Piotrovsky, for providing specimens and the artist of my laboratory Miss T. N. Steiker for preparing illustrations. Phillip C. Heemstra kindly provided comparative data on *P. rubiginosum* and donated a specimen of that species from South Africa. The manuscript was read by William D. Anderson, Jr., Bruce B. Collette, and Phillip C. Heemstra all of whom offered important suggestions for its improvement.

Literature Cited

Collette, B. B. & N. V. Parin. 1991. Shallow-water fishes of Walters Shoals, Madagascar Ridge.— Bulletin of Marine Science 48:1–22.

Duhamel, G. 1984. Ichtyofaune d'un haut-fond (34°54′S, 53°14′E) de l'ocean Indien sud-oest.— Cybium 8(4):91–94.

Eschmeyer, W. C. 1990. Catalog of the genera of Recent fishes. California Academy of Sciences, San Francisco, 697 pp.

Heemstra, P. C. & J. E. Randall. 1977. A revision of the Emmelichthyidae (Pisces: Perciformes).— Australian Journal of Marine and Freshwater Research 28:361–396.

P. P. Shirshov Institute of Oceanology, Academy of Sciences, Krasikova Ul. 23, Moscow 117218, USSR.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 468–473

MATSUBARICHTHYS INUSITATUS, A NEW GENUS AND SPECIES OF VELVETFISH (SCORPAENIFORMES: APLOACTINIDAE) FROM THE GREAT BARRIER REEF

Stuart G. Poss and G. David Johnson

Abstract.—*Matsubarichthys inusitatus* is described from a single specimen, taken from One Tree Island, Queensland, Australia. It is readily distinguished from other scorpaenoids by its unique dorsal-fin formula (II, IV, 6) and vertebral formula (9 + 12 = 21), both with fewer elements than previously reported for a scorpaenoid; a low anal fin-ray count (II,4); a pelvic fin-ray count of I,1; and the gill opening restricted to a pore dorsal to the opercle. Although the holotype is small (8.5 mm SL) and study of its internal anatomy thus limited, *Matsubarichthys inusitatus* is a relatively primitive aploactinid that can not be readily assigned to either of the two currently recognized aploactinid subfamilies, but may be a sister-group of the Bathyaploactininae.

Neuston tow sampling conducted at One Tree Island at the southern end of the Great Barrier Reef resulted in the capture of a single predemersal-staged specimen representing a new genus and species of Aploactinidae (velvetfishes).

Aploactinids, of which 36 have been previously described, are widely distributed throughout the Indo-Pacific. However, many remain extremely rare in collections and thus poorly understood. Although it is evident that velvetfishes are closely allied with the scorpionfishes, particularly the stonefishes and waspfishes (Matsubara, 1943a), the combination of presumptively uniquely derived characters used to define the family presents conflicting hypotheses of relationship. This paper describes an aploactinid scorpaenoid whose features underscore this conflict.

Materials and methods.—Counts and head spine terminology used in this paper follow those of Eschmeyer (1969). Measurements were taken as specified in Poss (1982), but using an ocular micrometer instead of dial calipers. Illustration of the axial skeleton was based on multiple radiographs using Olympus SZH and Leitz Stereo TS binocular dissecting microscopes.

Radiographic techniques suggested by Tucker and Laroche (1984) were followed. Radiographs were taken on a Koizumi Softex SE X-ray unit, using Kodak ultrafine grain SB single emulsion diagnostic radiographic film and Kodak Industrex R type film. Exposure times of 6 to 12 sec at 50 to 70 kv and 3 mA were employed.

The specimen was lightly stained with alizarin red S in 70% ethanol to show more clearly critical osteological features not visible in the radiographs. The bones stained only weakly, probably the result of prolonged storage in unbuffered formalin prior to transfer to ethanol.

The abbreviation AMS designates the Australian Museum, Sydney, where the holotype and only specimen is deposited.

Matsubarichthys, new genus
Figs. 1, 2

Type species.—*Matsubarichthys inusitatus.*

Diagnosis.—An aploactinid scorpaenoid fish with: dorsal fin II, IV, 6; anal fin II, 4;

pelvic fin I, 1; 15 pectoral fin-rays; fin rays in all fins unbranched; no enlarged preorbital spines; no scales (except for lateral line); branchiostegal membranes connected to isthmus along entire length, opening to opercular chamber restricted to a small pore above tip of opercle; no slit behind posteriormost hemibranch; no pterygiophore inserting between neural spines of sixth and seventh vertebrae.

Matsubarichthys inusitatus can be distinguished readily from all other scorpaenoid fishes by its dorsal-fin, pelvic-fin, and vertebral counts, which are lower than those of any other species in the suborder.

Description.—Head large (Fig. 1), without extensive spination. Lacrimal (infraorbital 1), immovable, its posteroventral border with 2 small, weak spines. Infraorbital bones 2 and 3 strongly arched, with large infraorbital canal pores opening as distinctly raised tubes. Small, tubular, fourth infraorbital bone present. Nasal bone tubular, without spine. Anterior nostril, an attenuate tube near tip of snout, extends over premaxilla. Interorbit wide, with ascending processes of premaxillae extending between anterior half of orbits. Mouth strongly upturned. Teeth on upper and lower jaws; none on palatines. Presence of teeth on vomer uncertain. No slit behind posteriormost hemibranch. One infrapharyngobranchial tooth plate. Epibranchial of first gill arch with a narrow, notably short uncinate process extending posteromedially from dorsal ramus of bone at an angle of about 90°. Three lateral-line pores on each side on lower jaw, a fourth between lower jaw and preopercle on each side. Interhyal narrow throughout its length, not expanded posteriorly. Branchiostegal rays 6. Posterior opening of opercular chamber restricted to a small pore above tip of opercle, with branchiostegal membranes firmly attached to isthmus. Ventral surface of urohyal narrow. No pseudobranch.

Body covered with smooth skin, naked, except for lateral line. Swimbladder not visible in radiograph, probably absent. First two dorsal-fin pterygiophores enlarged and closely associated with cranium, both inserting in first interneural space; first dorsal spine in supernumerary and second in serial association with first pterygiophore, both spines enlarged and robust, the second notably so; third pterygiophore inserting in fourth interneural space and bearing no supernumerary spine (Fig. 2). Neural spines of first two vertebrae small, directed forward, but not clearly visible in radiographs. Neural spines of sixth and seventh vertebrae without interdigitating dorsal-fin pterygiophore. Caudal skeleton with parhypural and hypurals 1, 2, 3, and 4 fused into single plate and to urostyle (hypural 5 not visible in radiograph); neural spine of preural centrum wide and long; number of epurals and uroneurals not determinable.

Etymology.—Named in honor of the late Professor Kiyomatsu Matsubara, in recognition of his pioneering and inspiring research on scorpaenoid fishes. The gender is masculine.

Matsubarichthys inusitatus,
new species
Figs. 1, 2

Holotype.—AMS I.29395-001, 8.5 mm standard length (SL). Australia, Queensland, Great Barrier Reef, Capricorn Group, One Tree Island, 23°30′S, 152°05′E, neuston tow, Patti D. Schmitt, date, time, and depth of capture unknown.

Description.—Dorsal fin-rays II, IV, 6. Anal fin-rays II, 4. Pectoral fin-rays 15 right, 15 left. Caudal fin damaged, but relatively long and rounded, without branched rays; 10 segmented rays (5 ventral; 5 dorsal), and 4 unsegmented, procurrent rays (2 dorsal; 2 ventral). Lateral line with 6 long, tube-like scales, the first 3 very close together, the last extending over base of caudal fin. Gill rakers 1 + 4 = 5 (right). Vertebrae: 9 precaudal + 12 caudal = 21.

Head extremely large; notably depressed

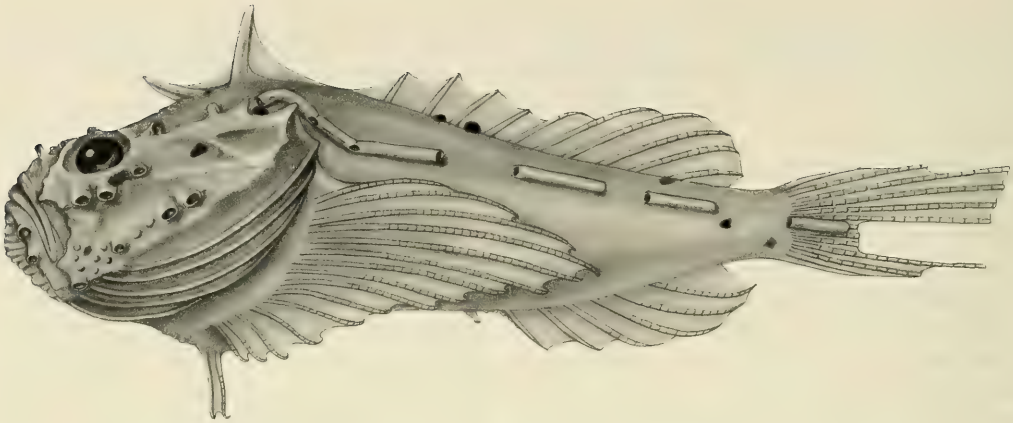


Fig. 1. Holotype of *Matsubarichthys inusitatus* in lateral view (AMS I.29335-001, 8.5 mm SL). Broken tip of second dorsal fin spine reconstructed.

(specimen with buccal cavity strongly flared laterally on preservation). Lacrimal with small spinous points, but without enlarged spines or strong ventral lobes. Preopercle with 2 short, somewhat blunt spines near posterior margin of third infraorbital bone, the more dorsal the larger; additional, more ventrally located spines, if present, not visible through skin. Cheek with a few fleshy protuberances. Similar warty structures scattered over ventral surface of head.

Body scales absent, except for lateral line. Lateral-line scales extremely long, distinctly tubular. The first 3 touch each other and appear, without high magnification, as a single elongate scale, except for presence of pores demarking their ends.

Dorsal fin originates above dorsal arm of preopercle, with anteriormost two spines well separated from remainder of fin; the first locked and directed anteriorly, the second more robust, also locked, but directed vertically. Second spine broken (reconstructed in Fig. 1). Third and succeeding spines relatively narrow.

Color in life unknown. Color of specimen, now in 70% ethanol, uniformly buff tan with several conspicuous, densely melanic inclusions that form distinct, deep-to-superficial spots, most bilaterally symmetric: largest, about ¼ to ⅓ size of pupil in ventral well of orbit just dorsal to third infraorbital bone; another smaller spot deep and immediately ventral to opercular-hyomandibular hinge; a smaller inclusion just dorsal to opercular opening, and a still smaller spot anterior to this; two small spots on each side posterior to symphysis of premaxillae; large spot on left side of isthmus; several minute dark spots over ventral surface of iris, one lateral to urostyle. Small, densely melanic spots at bases of dorsal-fin spines, one between base of first and second, one posterior to fourth, and a more conspicuous one posterior to fifth spine; spot anterior to anal-fin origin; another near base of last dorsal-fin ray (right side only); one in axil of left (but not right) pectoral fin.

Measurements for the holotype in mm are as follows (percent SL in parentheses): standard length 8.5, head length 3.7 (44); snout 0.8 (9); orbit 1.0 (12); interorbit 1.0 (12); jaw 1.4 (16); postorbit 2.0 (24); body depth 3.1 (36); predorsal 2.2 (26); anal fin 2.9 (34); caudal fin 1.6 (19); pectoral fin 3.1 (36); pelvic fin 0.6 (7); dorsal spines, first 0.7 (8), second 0.9 (11), third 0.3 (4), fourth 0.6 (7), fifth 0.7 (8), sixth 0.7 (8); anal spines, first 0.8 (9), second 1.1 (13); width of interorbital ridge 0.4 (5); caudal peduncle depth 0.9 (11); snout to second dorsal spine 2.3 (27), to third dorsal spine 4.0 (47), to fourth dorsal

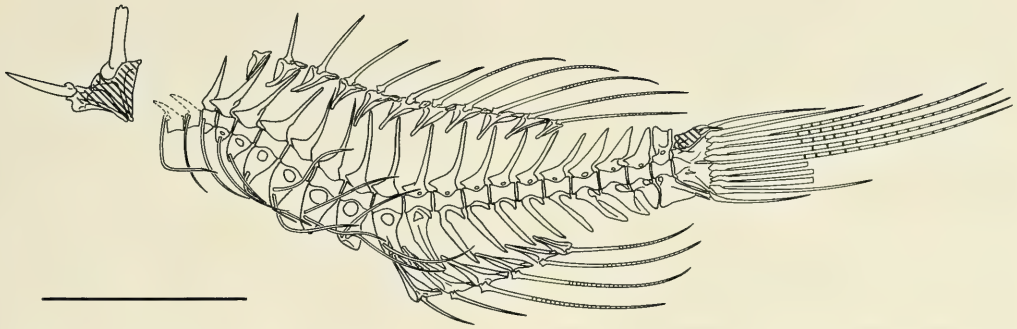


Fig. 2. Axial skeleton of holotype of *Matsubarichthys inusitatus* as reconstructed from multiple radiographs. Neural and haemal spines are not autogenous. Shape of anterior pterygiophores and epural region of caudal skeleton (indicated by hatching) cannot be determined from radiographs. Bar represents 2.0 mm.

spine 4.4 (52), to fifth dorsal spine 4.7 (55), to pelvic-fin insertion 3.0 (35); width of first dorsal spine at midlength 0.2 (2); depth of interorbit at midorbit 0.1 (1); incision of fin membrane at fourth dorsal spine from tip to membrane 0.1 (1); opercular tip to dorsal fin 0.7 (8); uppermost preopercular spine 1.0 (12); first dorsal spine to fifth dorsal spine 3.1 (36), to pelvic-fin insertion 2.8 (33), to anal-fin origin 4.5 (53); fifth dorsal spine to pelvic-fin insertion 4.0 (47), to last dorsal spine 0.9 (11), to anal origin 2.2 (26); last dorsal spine to last dorsal ray 2.3 (27), to pelvic insertion 4.0 (47), to last anal ray 2.4 (28), to anal origin 2.0 (24); last dorsal ray to last anal ray 1.2 (14), to anal origin 2.4 (28); anal-fin origin to last anal ray 1.9 (22); pelvic-fin insertion to anal-fin origin 3.2 (38).

Distribution.—Known only from the holotype taken near the southern end of the Great Barrier Reef at One Tree Island, Capricorn Group, Queensland, Australia.

Etymology.—The Latin specific epithet, *inusitatus,* means unusual or rare.

Comparisons.—A pelvic fin with only one spine and a single soft ray (I,1) is known to occur among scorpaenoids only in atypical specimens of the aploactinids *Erisphex pottii* and *Kanekonia florida.*

Distinct, densely melanic spots on the head are unusual among scorpaenoids. It is likely that their presence in our specimen is a transitory larval/juvenile character but this cannot be verified until larger specimens are collected. Large tubular lateral-line scales occur commonly in *Cocotropus*-stem scorpaenoids. Those of *Matsubarichthys inusitatus* are particularly large, but this exaggerated size may reflect a juvenile condition. In the tetrarogine *Coccotropsis gymnoderma,* which also has very large tubular lateral-line scales, those of very small specimens appear disproportionately large. Conspicuous cephalic lateral-line pores are present in the aploactinid *Prosoproctus pataecus* (see Poss & Eschmeyer, 1979). Distinctly tubed head pores occur in a number of aploactinids, for example *Xenaploactis anopta* (see Poss & Eschmeyer, 1980).

Discussion.—The precise limits of the Aploactinidae and the details of their phylogeny are uncertain due to the high degree of morphological differentiation and considerable character incompatibility among specialized features otherwise useful in characterizing velvetfishes. Matsubara (1943a, 1943b) defined the aploactinids (as a subfamily Aploactinae [sic] of the Scorpaenidae) based on the close association of the anteriormost two dorsal spines with the cranium, their separation from succeeding dorsal spines, a highly reduced suspensorium, and lack of a supraoccipital crest (neither of the latter two features readily visible from radiographs of *Matsubarichthys inusitatus*). These features probably are not

uniquely derived among scorpaenoids and do not characterize all aploactinids. Among scorpaenoids it is typical for a single pterygiophore to insert between each successive pair of neural spines, except the anteriormost. However, among all species assigned to the Aploactinidae as delimited by Poss & Eschmeyer (1978), a single pair of neural spines, invariably of vertebrae 6–8, have no interdigitating pterygiophore.

A combination of presumably specialized, but not uniquely derived, features readily distinguishes aploactinids from other scorpaenoid fishes. These include the total absence of branched fin rays, notably tubular and often highly ornamented lateral-line scales, non-spinous, tubular nostrils, pelvic fins with 1–3 soft rays, no slit behind the 4th gill arch, a single infrapharyngobranchial tooth plate, no palatine teeth, typically blunt as opposed to pungent head spines, and atypical, tack-like, pseudocycloid or ctenoid scales, when scales are present. These features also place *Matsubarichthys inusitatus* within the Aploactinidae.

Matsubarichthys inusitatus can not, however, be assigned unequivocally to either aploactinid subfamily. *Matsubarichthys inusitatus* is unlike members of the Aploactininae in lacking a unique papillose extension near the isthmus that forms a seal between the otherwise separate isthmus and branchiostegal membranes (Poss & Eschmeyer 1978). Although *M. inusitatus* shares a highly restricted gill slit and a narrow posterior margin of the interhyal with members of the Bathyaploactininae, it lacks the greatly enlarged and highly movable first infraorbital bone, rather spatulate head spines, and characteristic orientation, shape, and reduced size of the opercle that characterize the two bathyaploactine genera *Acanthosphex* and *Bathyaploactis*. Interestingly, the first epibranchial of *Matsubarichthys inusitatus* bears a much reduced posteromedially directed uncinate process similiar to that of *Acanthosphex leurynnis* and *Kanekonia florida*. *Matsubarichthys* may prove to be the sister-group of the bathyaploactines. If so, the shapes of the highly mobile, complex, and variously spined lacrimals seen in both aploactinines and bathyaploactines, and especially useful in diagnosing the genera, may be quite plastic phylogenetically.

As Poss & Eschmeyer (1979) pointed out, it is difficult to argue that the presence of restricted gill slits resulting from fusion of the branchiostegal membranes to the isthmus is uniquely derived among scorpaenoids (these authors erroneously included *Gnathanacanthus goetzeei* among scorpaenoid species with restricted gill openings). Nonetheless, the combination of features associated with this fusion that occurs in all members of the Synanceiinae (sensu Eschmeyer & Rama Rao 1973 and including Erosinae of Matsubara 1943a, 1943b), the Minoinae, the Choridactylinae (sensu Eschmeyer et al. 1979), and some aploactinid scorpaenoids, may indicate common ancestry. Many species of these lineages possess extremely large heads (greater than 40% SL), enlarged and variously mobile lacrimal spines, anterior neural spines in the region of precaudal vertebrae 5 to 8 that are notably thinner and more delicate than the others, a long and expanded neural spine on the first preural centrum, a strongly consolidated caudal skeleton with a reduced number of caudal fin-rays, palatines without teeth, a single bilaterally symmetric pair of infrapharyngobranchial tooth plates (except *Inimicus* spp. and *Erosa erosa,* which have two bilaterally symmetric pairs, albeit the anterior pair substantially reduced in the latter genus), and loose, virtually naked skin (lateral-line scales and vestigial scales in a few species excepted).

Like other aploactinids, *M. inusitatus* is more specialized than the synanceiines, choridactylines, and minoines, at least in having one pair of consecutive neural spines (6 and 7 in *M. inusitatus*) of the precaudal vertebrae that lacks an intervening dorsal pterygiophore. Like some aploactinids, the

anterior nostril is far forward on the snout. The combination of character states in *M. inusitatus* results in incompatibility among shared, derived characters that would otherwise be useful in establishing the cladistic relationships of the relatively advanced members of the *Cocotropus* stem. Another rare scorpaenoid, *Eschmeyer nexus,* which exhibits a number of features discussed above (Poss & Springer 1983), poses similar problems. Additional specimens of *Matsubarichthys inusitatus* and other extremely rare basal aploactinids are needed for more rigorous analyses.

Acknowledgments

We thank J. Leis of the Australian Museum for kindly making this unique specimen available to us and L. Knapp for delivering it. We further thank V. G. Springer and W. N. Eschmeyer for review of this manuscript. JoEllen Trecartin is acknowledged for illustrating the holotype and Sara LeCroy for rendering its axial skeleton. This work was supported, in part, through an NSF grant (BSR 8705373) to SGP.

Literature Cited

Eschmeyer, W. N. 1969. A systematic review of the scorpionfishes of the Atlantic Ocean (Pisces: Scorpaenidae).—Occasional Papers of the California Academy of Sciences 79:1–130.

———, & K. V. Rama-Rao. 1973. Two new stonefishes (Pisces, Scorpaenidae) from the Indo-West Pacific, with a synopsis of the subfamily Synanceiinae.—Proceedings of the California Academy of Sciences 39(18):337–382.

———, ———, & L. E. Hallacher. 1979. Fishes of the scorpionfish subfamily Choridactylinae from the Western Pacific and Indian Ocean.—Proceedings of the California Academy of Sciences 41(21):475–500.

Matsubara, K. 1943a. Studies on the scorpaenoid fishes of Japan. Anatomy, phylogeny and taxonomy (I).—Transactions Sigenkagaku Kenkyusyo 1:1–170.

———. 1943b. Studies on the scorpaenoid fishes of Japan. Anatomy, phylogeny and taxonomy (II).—Transactions Sigenkagaku Kenkyusyo 2: 171–486.

Poss, S. G. 1982. A new species of the aploactinid fish genus *Kanekonia* from Halmahera, Indonesia and a redescription of *Kanekonia florida.*—Japanese Journal of Ichthyology 28(4):1–6.

———, & W. N. Eschmeyer. 1978. Two new Australian velvetfishes, genus *Paraploactis* (Scorpaeniformes: Aploactinidae), with a revision of the genus and comments on the genera and species of the Aploactinidae.—Proceedings of the California Academy of Sciences 41(18):401–426.

———, & ———. 1979. *Prosoproctus pataecus,* a new genus and species of velvetfish from the South China Sea (Aploactinidae: Scorpaeniformes).—Japanese Journal of Ichthyology 26:11–14.

———, & ———. 1980. *Xenaploactis,* a new genus for *Prosopodasys asperrimus* Gunther (Pisces: Aploactinidae), with description of two new species.—Proceedings of the California Academy of Sciences 48:287–243.

———, & V. G. Springer. 1983. *Eschmeyer nexus,* a new genus and species of scorpaenid fish from Fiji.—Proceedings of the Biological Society of Washington 96:309–316.

Tucker, J. W., & J. L. Laroche. 1984. Radiographic techniques in studies of young fishes. Pp. 37–39 *in* H. G. Moser et al., eds., Ontogeny and systematics of fishes. Special Publication No. 1, American Society of Ichthyologists and Herpetologists.

(SGP) Gulf Coast Research Laboratory, P.O. Box 7000, Ocean Springs, Mississippi 39564; (GDJ) Department of Vertebrate Zoology (Fishes), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 474–492

STUDIES OF NEOTROPICAL CADDISFLIES, XLVI: THE TRICHOPTERA OF THE RÍO MOCHE BASIN, DEPARTMENT OF LA LIBERTAD, PERU

Oliver S. Flint, Jr. and Luis Reyes A.[1]

Abstract.—Twenty-four species are recorded from the Río Moche (primarily) and Río Saña basins of northwestern Peru. The climatological, chemical, and life zone characteristics of the Río Moche are discussed. Six species are described as new: *Chimarra* (*C.*) *dolabrifera, C.* (*Curgia*) *otuzcoensis, Smicridea* (*Rhyacophylax*) *bidactyla, Hydroptila sicilicula, Neotrichia riparia,* and *Triaenodes peruanus.* The trichopterous fauna of this region is basically one of widespread species, some known from the U.S.A. to Chile.

The trichopterous fauna of Peru, the third largest country in South America, is very poorly known. There have been very few studies dealing exclusively with Peru, and these are limited to very restricted portions (Martynov 1912; Roback 1966; Flint 1975, 1980), thus most Peruvian records are scattered throughout the literature. Reyes has compiled a list of 107 species recorded from Peru (including those newly reported in this paper), which is certainly but a small fraction of the number of species that must occur there. Essentially nothing has been recorded from the coastal and immediately adjacent montane zones of northern Peru. This is the first report on the Trichopterous fauna that may be expected in other such suitable sites in these dry regions of western South America. Material on which this study is based is deposited in the National Museum of Natural History (NMNH), Washington and the Museo de Historia Natural "Javier Prado," Lima, Peru.

Río Moche Basin

The Río Moche basin is wholly located in the Department of La Libertad on the northwestern coast of Peru, the river entering the Pacific Ocean just south of Trujillo, its capital (Fig. 1). The drainage basin is about 96 km deep, widening to about 25 km at the ocean, and covering 2708 square km. It is situated between parallels 7°46′ and 8°15′ South and between meridians 78°16′ and 79°08′ West.

The river itself is 102 km long with an average gradient of 4% (this and the following information is extracted primarily from Anonymous 1973, 1987). Its origin is in the Laguna Grande at 3988 m elevation, near the town of Quiruvilca in the Province of Santiago de Chuco, from which it flows through the Provinces of Otuzco and Trujillo (Fig. 2). Just below the town of Simbal, at 576 m, it is joined by the Río Sinsicap, which originates above the village of Sinsicap at over 3000 m. Most of the collections were made in the portion of the Río Sinsicap between Simbal and the junction with the Río Moche. This section of the river is called by local inhabitants the Río Lucumar (Figs. 3, 4) and it divides into several arms, which reunite near the village of Cumbray at which point it takes the name of Cumbray Creek (Figs. 5, 6) and serves as the laundry area for the small village.

The rains in the basin are concentrated from January to April, with the driest period from June to September. The average

[1] Please see postscript.

Fig. 1. Map showing the placement of the Río Moche basin (stippled) in the Department of La Libertad, its provincial subdivisions and its position in Peru.

annual rainfall in the littoral is about 10 mm, rising perhaps to 100 mm at Simbal (average annual rainfall at nearby Samne, 1450 m is 162 mm), and to near 1500 mm at the river's origin (average annual rainfall at Quirivilca is 1389 mm). During low water flow the Río Lucumar near Simbal is 1–1.5 m wide by 30–50 cm deep (Fig. 3), increasing to 2.5 m by 50–70 cm in the rainy season (Fig. 4). The Cumbray Creek section is a bit larger, in the dry season 1.5 m by 50 cm (Fig. 5) but 3 m by 60–80 cm in the wet (Fig. 6). Much of the water of the lower Río Moche is diverted for irrigation, but at Puente Moche the river still runs 3–4 m by 50–80 cm in the dry season and 12–15 m by 1 m in the rainy season. An analysis of the water of Cumbray Creek gives a pH of 7.5, conductivity of 0.78 mmhos/cm, sum of cations 9.2 meq/l (Ca 4.2, Mg 2.6, Na 2.4, K 0.05), sum of anions 9.2 meq/l (CO_3 0, HCO_3 3.5; NO_3 0, SO_4 4.5, Cl 1.2).

The Río Moche over its course passes through five Holdridge life zones (Tosi 1960). It arises in "pradera muy húmeda montano (pmh-M)" which has an annual rainfall of 1000–1400 mm, passing at approximately 3700 m into the "pradera hú-

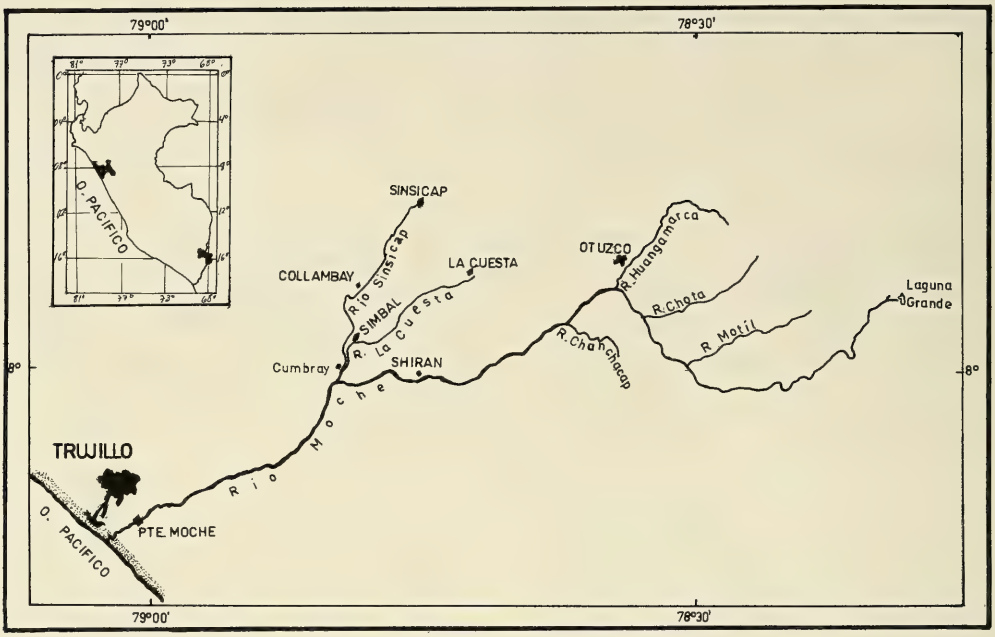
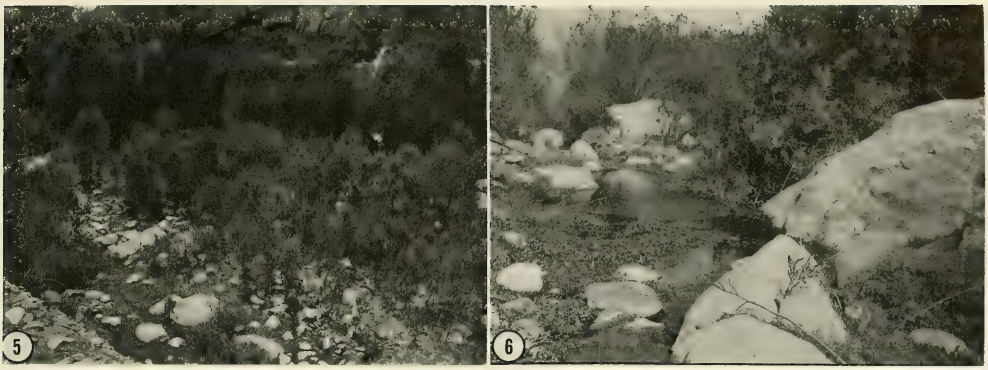


Fig. 2. Details of the Río Moche, its tributaries and principal towns.

meda montano (ph-M)" which lies in an annual rainfall regime of 500–1000 mm. Between elevations of 1600–2800 m, with annual rainfalls in the range of 200–500 mm the river flows in the "estepa espinoso montano-bajo (ee-MB)" zone. In the zone of Simbal and Cumbray Creek, where most of the collections were made, at elevations of 500–1800 m and rainfalls of 50–200 mm the life zone is denoted as "matorral desértico pre-montano (md-PM)." Puente Moche is situated below this zone in the "desierto pre-montano (d-PM)," which runs to the mouth of the river with rainfall between 0–50 mm.

The streamside vegetation at Cumbray Creek is dominated by *Baccharis* sp. (Fig. 5), with other typical plants of this zone: *Cereus macrostibas, Cereus candelaris, Capparis* sp., and *Caesalpinia* sp. Typical plants of the coastal zone are: *Capparis* spp., *Crytocarpus* sp., *Acacia macracantha,*

Figs. 3–4. Río Lucumar, near Simbal, site of the collections of *Triaenodes peruanus*: 3, dry season, June 1988; 4, wet season, January 1989.



Figs. 5–6. Cumbray Creek section, near Cumbray: 5, dry season, showing *Baccharis* the principal component of the flora, June 1988; 6, wet season, January 1989.

Arundo donax, Ginerium oleander, Schinus molle, Tessaria integrifolia, Baccharis sp. and *Ludwigia* sp.

Distribution

Figure 7 shows the known distributions of the twenty-four species of Trichoptera taken in this survey that could be specifically determined. Four of the species are recorded only from the Río Moche basin, while three additional species are known with certainty only from adjacent Ecuador or Peru. However, the majority are distributed into Central America, Mexico or even to the U.S.A. or the West Indies and a few are also known to live as far south as Argentina or Chile.

Thus, it seems that the somewhat depauperate trichopterous fauna of the Río Moche Basin, at least up to 500–600 m, is one with most species having a wide distribution in Central America and northern South America. We predict that the apparently endemic species will be found to exist as far north as Ecuador and south perhaps to central Peru, if not farther. The fauna here reported will probably be found in similar coastal river systems between central Ecuador and central Peru.

Family Hydrobiosidae
Atopsyche species 1

This is a very large genus of over 100 described species, limited exclusively to the Americas, including the Greater Antilles and the southwestern United States. Nine species have been recorded from Peru, but undoubtedly many more will be found with more extensive collecting. The cleared genitalia of the examples taken in this survey reveal two very distinctive species, but they cannot be specifically identified as males are lacking.

Species 1 is known only from larvae and a female metamorphotype, thus its wing length and general coloration are unknown.

Species \ Dist.	U. S. A.	Mexico	Cent. Amer.	Colombia	Venezuela	W. Indies	Ecuador	Saña/Moche	Peru	Argentina	Chile
Protoptila tojana		x	x				x	x	x		
Protoptila orotina				x				x			
Chimarra dolabrifera							x	x			
Chimarra emima			x	x			x	x			
Chimarra otuzcoensis								x			
Polycentropus joergenseni				x	x		x	x	x	x	
Smicridea bivittata		x	x	x	x		x	x			
Smicridea saucia								x	x		
Smicridea murina			x	x			x	x	x	x	x
Smicridea bidactyla					?		x	x			
Zumatrichia palmara			x				x	x			
Hydroptila constricta		x	x	x				x			
Hydroptila ditalea		x				x	x	x			
Hydroptila grenadensis			x	x		x	x	x			
Hydroptila sicilicula								x			
Neotrichia riparia								x			
Neotrichia gotera								x		x	
Ochrotrichia tenanga		x	x		x			x			
Ochrotrichia malada				x				x			
Oxyethira parce	x	x	x	x	x		x	x	x	x	
Nectopsyche spiloma	x	x	x				x	x			
Nectopsyche punctata		x	x	x	x		x	x	x	x	
Triaenodes peruanus								x			
Helicopsyche vergelana		x	x	x	x			x			

Fig. 7. Known distributions of the identified species of caddisflies collected in the Río Moche and Río Saña basins.

The general body size of the pupa would indicate that it is quite a bit smaller than the following species, perhaps with a forewing length of only 10 mm.

Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar-Cumbray Creek, 17 Sep 1989, L. Reyes A., 2 larvae, 3 prepupae, 3 pupae, 1 ♀ metamorphotype.

Atopsyche species 2

This species, only known from a single female, has a forewing length of 13 mm and a dark coloration.

Material.—Peru, Dept. La Libertad, Prov. Otuzco, Dist. Otuzco, Río Pollo, Otuzco, 2620 m, 1 Jul 1989, L. Reyes A., 1 ♀.

Family Glossosomatidae

Protoptila tojana Mosely

Protoptila tojana Mosely, 1954:331.—Flint, 1963:476.—Maes & Flint, 1988:2.

The species was described from southern Mexico, and recorded from Honduras, Nicaragua, Costa Rica and Lima, Peru, thus exhibiting the greatest known range of any species in the genus. There is additional material from Guatemala, El Salvador, Panama and Ecuador in the NMNH. Its presence in northern Peru is, therefore, not surprising. In addition to the adults, larvae, pupae, and male and female metamorphotypes have been taken.

Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 11–12 Dec 1987, L. Reyes A., 4 ♂; 24 Jun 1988, 3 ♂, 1 ♀; 6 Jul 1989, 14 ♂, 1 ♀; 22 Jul 1989, 29 ♂, 2 ♀; 5 Sep 1989, 5 ♂. Río Lucumar, Cholocar, 17 Sep 1989, 1 ♂. Río Lucumar-Cumbray Creek, 15 Apr 1988, 1 ♂. Dist. Laredo, Río Moche, Conache, 28 Jul 1989, 6 ♂, 4 ♀. Dist. Moche, Río Moche near Puente Moche, 18 Jul 1989, 6 ♂, 4 ♀. Dept. Lambayeque, Río Saña, Oyotún, 200 m, 18 Nov 1989, 7 ♂.

Protoptila orotina raposa Flint

Protoptila orotina raposa Flint, 1974a:13.

This subspecies was described from the wet Pacific coast of Colombia; this is the second known occurrence of the subspecies. The nominate subspecies is found widely along the drier Pacific coast of Costa Rica and Panama.

Material.—Peru, Dept. Lambayeque, Río Saña, Oyotún, 200 m, 18 Nov 1989, L. Reyes A., 9 ♂.

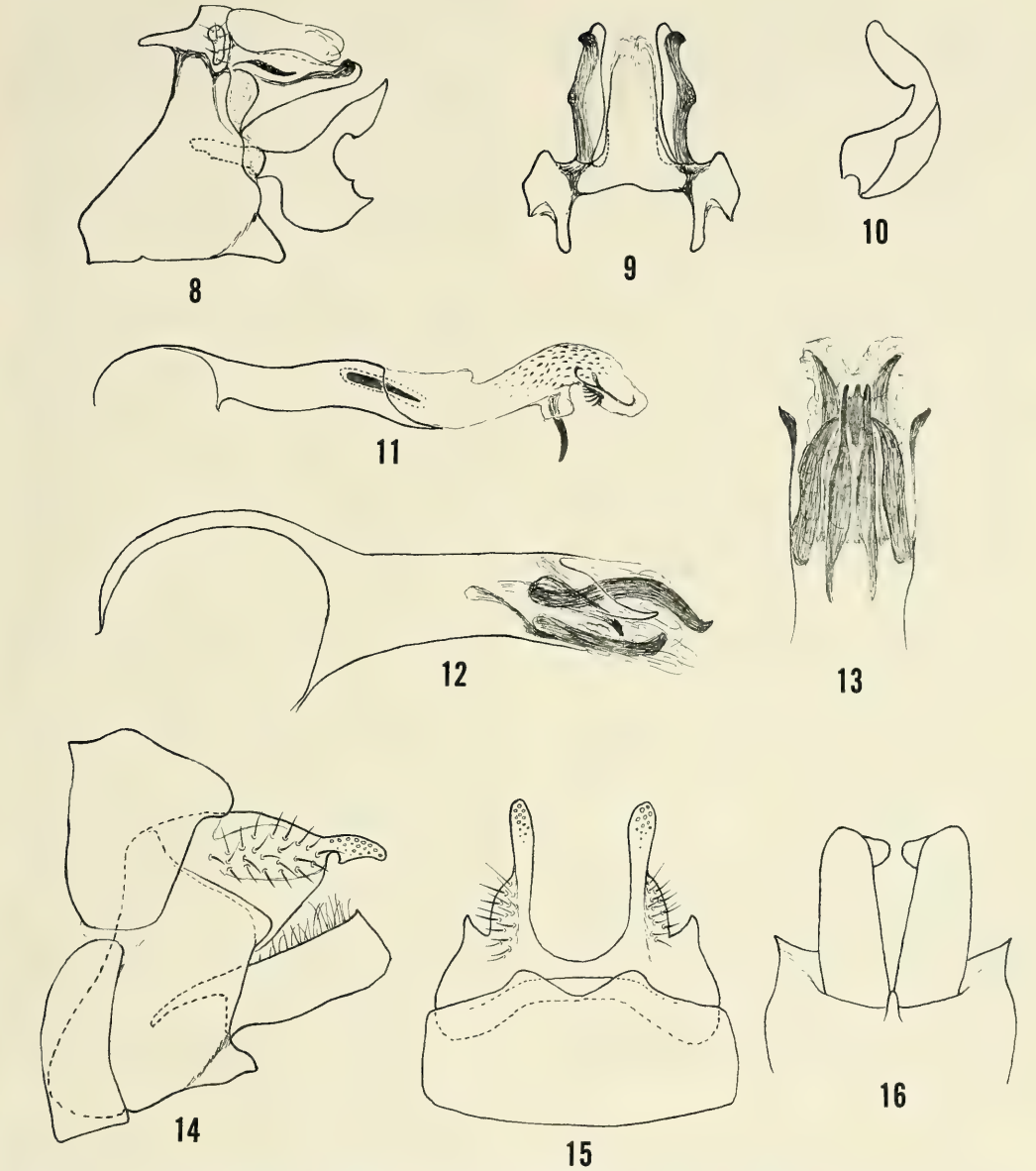
Family Philopotamidae

Chimarra (*Chimarra*) *dolabrifera*, new species

Figs. 8–11

This species is closely related to *C. platyrhina* Flint from Venezuela. It is recognized by differences in the tenth tergites and claspers of the male genitalia. The tenth tergite in *C. platyrhina* is slightly upturned apically in lateral aspect and only slightly expanded in dorsal aspect; in *C. dolabrifera* the tergite is straight apically with a distinct dark projection subapically which in dorsal aspect is seen to be a sharp point directed laterad. The clasper of *C. dolabrifera* in posterior aspect has its dorsal process developed into a distinct mesal lobe which in *C. platyrhina* is totally lacking.

Adult.—Length of forewing, 4.5 mm. Color overall fuscous, unicolorous; legs basally a bit paler. Forewing with a bulla on Rs; hindwing with 4 branches to Rs and 3 to M. Male genitalia: Ninth segment with anterior margin produced ventrolaterally, with a short dorsolateral process; posteroventral process triangular in outline, about as long as wide basally. Tenth tergum with a pair of elongate mesal plates, most heavily sclerotized along dorsal margin; lateral plate elongate, tapering apicad with a midlateral more strongly sclerotized ridge ending in a dark knob subapically, in dorsal aspect this knob is produced as a sharp laterally-di-



Figs. 8–16. Male genitalia of *Chimarra*. 8–11, *C. dolabrifera*: 8, lateral; 9, ninth and tenth terga, dorsal; 10, clasper, posterior; 11, phallus with endotheca everted, lateral. 12–16, *C. otuzcoensis*: 12, phallus, lateral; 13, apex of phallus, dorsal; 14, lateral; 15, eighth, ninth and tenth terga, dorsal; 16, ninth sternum and claspers, ventral.

rected point and the ridge expanded at mid-length. Clasper with a broad, scooplike ventral portion and an apicodorsal process elongate and narrow in lateral aspect, but bearing a distinct mesal expansion in posterior aspect. Phallus with an apicoventral spine, a pair of subequal internal spines, a slender rod and ring assembly, and a dark spiculate pouch with a small sclerite bearing a cluster of small spines.

Material.—Holotype, male: Ecuador, Prov. Pichincha, Río Palenque Biological Station, 47 km S Santo Domingo de los Colorados, 750 m, 29 Jul 1976, J. Cohen, NMNH. Paratypes: Same data, 3 ♂; same, but 14 km E Santo Domingo de los Colorados, 5 Jul 1975, Langley & Cohen, 2 ♂; same, but 29 km W Santo Domingo de los Colorados, 6 May 1975, P. J. Spangler, 1 ♂. Prov. Los Ríos, Río Palenque Biological Station, 56 km N Quevedo, 220 m, 7 Jan 1978, P. J. Spangler, 1 ♂. Prov. Cotopaxi, 133 km W Latacunga, 1080 ft [327 m], 2 Jul 1975, Langley & Cohen, 6 ♂. Prov. Esmeraldas, La Union, 3 Feb 1979, J. J. Anderson, 1 ♂. Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 17 Jun 1988, L. Reyes A., 9 ♂, 3 ♀; same, but Río Lucumar-Cumbray Creek, 430 m, 10 Mar 1987, 6 ♂, 3 ♀; same, but 5 Sep 1987, 10 ♂, 4 ♀. Dist. Moche, Río Moche near Puente Moche, 12 Dec 1988, 1 ♂.

Chimarra (*Chimarra*) *emima* Ross

Chimarra (*Chimarra*) *emima* Ross, 1959: 172.—Flint, 1991.

The species was originally described from Panama, and since recorded from Nicaragua, Costa Rica, Colombia and Ecuador. This is the first record of the species from Peru.

Material.—Peru, Dept. Lambayeque, Río Saña, Oyotún, 200 m, 18 Nov 1989, L. Reyes A.,1 ♂, 1 ♀.

Chimarra (*Curgia*) *otuzcoensis,* new species
Figs. 12–16

Within the New World species of *Chimarra* this species is placeable no further than to subgenus. The genitalia offer two previously unknown character states: the cercus is at first sight lost, but it would appear to have completely fused with the lateral surface of the tenth tergum and to be represented by a distinctly setate area, and, secondly, the tenth tergum is deeply divided mid-dorsally with the lateral portions narrow and rodlike. The armature internally at the apex of the phallus is also very different from anything seen in congeneric species.

Adult.—Length of forewing, 7–8.5 mm. Color overall jet black, immaculate. Forewing without bulla in the radial system; hindwing with 4 branches to Rs and 3 to M. Male genitalia: Eighth sternum narrow, parallel-sided, posterior margin concave; tergum produced posteriad into a pair of rounded, submesal lobes. Ninth segment produced into a rounded anteroventral lobe; with a small posteromesal keel; posterolateral margin slightly produced and angulate at midlength. Cercus apparently completely fused to lateral surface of tenth tergum, apparent only as a setate area. Tenth tergum in lateral aspect broad basally, produced into an apical, noselike lobe with many sensillae; in dorsal aspect with a deep, U-shaped, mesal excision separating lateral arms. Clasper elongate, rectanguloid with a small apicodorsal point in lateral aspect, in ventral aspect with an apicomesal lobe from dorsal margin. Phallus tubular, inflated basally; apex with a thin, pointed process from dorsolateral surface on each side; a pair of long, arched, black spines dorsally, and a shorter pair of black spines laterally; midventrally with a large, black spine whose apex is trifid in ventral aspect and which bears a pair of slender basal processes.

Material.—Holotype, male: Peru, Dept. La Libertad, Prov. Otuzco, Dist. Sinsicap, Río Sinsicap, Sinsicap, 2000 m, 23 Sep 1989, L. Reyes A., NMNH. Paratypes: Same data, 15 ♂, 3 ♀.

Family Polycentropodidae

Polycentropus joergenseni Ulmer

Polycentropus Jörgenseni Ulmer, 1909:75.—Fischer, 1962:83.—Weidner, 1964:91.
Polycentropus colombiensis Banks, 1910:

160.—Fischer, 1962:67.—Flint, 1967:6 (new synonymy).

Polycentropus anomalus Navas, 1923: 201.—Fischer, 1962:66 (new synonymy).

This species is very widely distributed along the Andes Mountains of western South America. Examples have been seen from Argentina, Bolivia, Colombia, Ecuador and Venezuela; Peru is here added to the list.

The types of all three names have been studied by Flint. The male lectotype from Pedregal, Argentina, is in the Zoologische Staatsinstitut und Zoologisches Museum, Hamburg, Germany. A male syntype, bearing a Navas "Typus" label (and hereby designated the lectotype), of *P. anomalus* Navas from "La Granja (Alta Gracia) Prov. de Cordoba 1–8.IV.1920 C. Bruch" is in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina. The female holotype of *P. colombiensis* Banks, temporarily at the National Museum of Natural History, is property of the Museum of Comparative Zoology, Cambridge, Massachusetts. The genitalia of the lectotype of *P. anomalus* has been cleared and found to agree with that of *P. joergenseni* from western Argentina. The *P. colombiensis* female type also has been cleared and its genitalia compared with females associated with males of *P. joergenseni* from several different regions, and all found in agreement.

Material.—Peru, Dept. La Libertad, Prov. Otuzco, Dist. Sinsicap, Río Sinsicap, Sinsicap, 2000 m, 23 Sep 1989, L. Reyes A., 2 ♂, 2 ♀, 5 larvae, 2 pupae, 5 ♀ metamorphotypes.

Family Hydropsychidae
Smicridea (*Smicridea*) *bivittata* (Hagen)

Hydropsyche bivittata Hagen, 1861:291.

Smicridea (*Smicridea*) *bivittata* (Hagen).—Fischer, 1963:131; 1972:144.—Flint, 1974b:16; 1981:22.

This is a common, widespread species from Mexico south to Ecuador, and eastwardly across northern South America to Suriname; this is the first known record from Peru.

Material.—Peru, Dept. Lambayeque, Río Saña, Saña, 5 Nov 1989, L. Reyes A., 1 ♂.

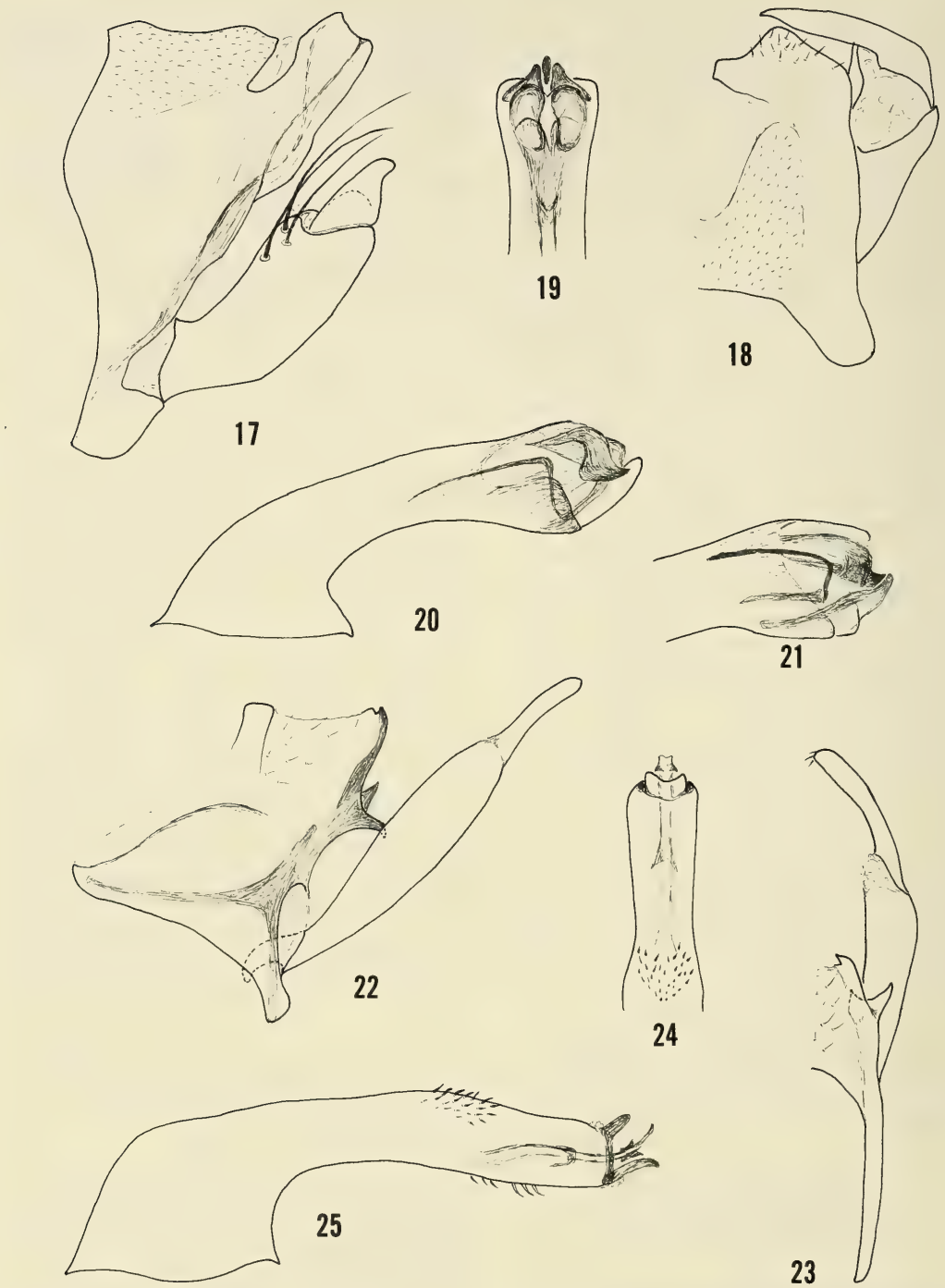
Smicridea (*Smicridea*) *saucia* McLachlan
Figs. 17–21

Smicridea saucia McLachlan, 1871:137.—Kimmins, 1957:106.—Fischer, 1963:134.

This species was originally described in 1871 from Peru "probably in the neighborhood of Lima," but has not been collected since. It is, therefore, with a great deal of pleasure that we record it again from Peru. Many years ago Flint borrowed the lectotype and 3 paralectotypes from the British Museum (Natural History), preparing drawings from them which are here published so that future workers may recognize the species. The examples from Trujillo Province are in complete agreement with the lectotype. However, the series from Otuzco are 1–2 mm larger (forewing length 6–7 mm as opposed to ca. 5 mm), and the sclerites at the tip of the phallus seem a bit different (Fig. 21). However, considering the overall similarity and lack of additional collections, they are considered conspecific for now.

The coloration of these fresh specimens are almost uniformly fuscous, with unmarked wings, the legs, however, are testaceous toward their bases.

Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar-Cumbray Creek, 27 Jun 1988, L. Reyes A., 1 ♀; 14 May 1989, 1 ♀; 21 May 1989, 1 ♂. Río Lucumar, Simbal, 8 Dec 1988, 1 ♀; 5 Sep 1989, 14 ♂, 6 ♀. Prov. Otuzco, Dist. Sinsicap, Río Sinsicap, Sinsicap, 2000 m, 23 Sep 1989, L. Reyes A., 9 ♂, 3 ♀.



Figs. 17–25. Male genitalia of *Smicridea*. 17–21, *S. saucia*: 17, lateral; 18, ninth and tenth terga and clasper, dorsal; 19, apex of phallus, dorsal; 20, phallus, lateral; 21, apex of phallus of specimen from Otuzco, lateral. 22–25, *S. bidactyla*: 22, lateral; 23, ninth and tenth terga and clasper, dorsal; 24, apex of phallus, dorsal; 25, phallus, lateral.

Smicridea (*Rhyacophylax*) *murina*
McLachlan

Smicridea murina McLachlan, 1871:137.—Fischer, 1963:134.
Smicridea (*Rhyacophylax*) *murina* McLachlan.—Flint, 1988:33.

This widespread species has an extensive synonymy (Fischer 1963, Flint 1988). It is known from Nicaragua in Central America south along western South America to central Chile. Although it is frequently found in wet, forested areas in Central America, it is equally at home in drier sites in waters open to the sun, perhaps explaining its success. Larvae and a female metamorphotype, probably of this species, have been taken in the Río Lucumar.

Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 11 Dec 1987, L. Reyes A., 2 ♂; same, but Río Lucumar-Cumbray Creek, 430 m, 2 Jul 1987, 1 ♂; 23 Aug 1987, 2 ♂. Dist. Moche, Río Moche at Puente Moche, 27 Jul 1988, 8 ♂. Dept. Lambayeque, Río Saña, Saña near the ruins of Corbacho, 30 Sep 1989, 4 ♂.

Smicridea (*Rhyacophylax*) *bidactyla,*
new species
Figs. 22–25

This distinctive species is a member of the *signata* group, closest to *S. signata* (Banks) itself, with which it shares the bilobed apicodorsal plate and ventral tonguelike lobe on the phallus. It differs in possessing a small apicodorsal point and large bifid ventrolateral process on the tenth tergum and lacking the lateral process on the phallus, but possessing a dorsal area and a midventral row of spinules in the same general phallic region. The examples from Venezuela differ in lacking the dorsal patch of spines on the phallus and having only a single strong process from the ventrolateral margin of the tenth tergum. It is expected that these examples will prove to be only a variation in the species.

Adult.—Length of forewing, 4–5 mm. Eye of male slightly enlarged, width middorsally ½ that of interocular distance. Color overall pale stramineous; forewing with faint dark marks along chord and over thyridial nygma, with a paler subterminal band. Anterolateral processes of fifth sternum of male nearly twice as long as sternum; without internal sacs. Male genitalia: Ninth segment with anterolateral margin produced into an angulate lobe, with a strong dorsolateral line. Tenth tergum membranous dorsomedially, apex sharply upturned and produced into a small point; ventrolateral margin strongly sclerotized, produced into an elongate, posterolaterally directed process bearing a shorter, mesally directed branch. Clasper with basal segment long, slightly inflated; apical segment with tip obliquely rounded in dorsal aspect. Phallus tubular, basal and apical sections meeting at nearly 90°; with a dorsolateral, saddle-shaped area of spines and midventral row of spines subapically; apex with a semierect, dorsal, bilobed plate and a narrow, ventral, tonguelike lobe; internal sclerite threadlike, slightly sinuous.

Material.—Holotype, male: Ecuador, Prov. El Oro, 6 km E Pasaje, 13 Jan 1978, P. J. Spangler & J. Anderson, NMNH. Paratypes: Same data, 22 ♂, 4 ♀. Río La Calera, Piñas/Zaruma, 19–20 Aug 1977, L. E. Peña G., 1 ♂, 1 ♀. Victoria/Arenillas, 18–19 Aug 1977, L. E. Peña G., 3 ♂, 30 ♀. Prov. Loja, Macara, 13 Aug 1977, L. E. Peña G., 10 ♂, 2 ♀. Río Puyango, 300 m, 17–18 Aug 1977, L. E. Peña, G., 11 ♂. Prov. Los Ríos, 11 km S Quevedo, 3 Jul 1975, Langley & Cohen, 3 ♂, 10 ♀. Prov. Pichincha, 29 km W Santo Domingo de los Colorados, 6 May 1975, Spangler et al., 7 ♂, 3 ♀. Peru, Dept. Lambayeque, Río Saña, near ruins of Corbacho, 30 Sep 1989, L. Reyes A., 4 ♂, 2 ♀. Other: Venezuela, Edo. Barinas, Río Santo Domingo, Barinas, 17 Feb 1976, C. M. & O. S. Flint, Jr., 2 ♂, 5 ♀.

Family Hydroptilidae

Zumatrichia palmara Flint

Zumatrichia palmara Flint, 1970:22.

The species was originally described from El Salvador and Costa Rica, but the collection at the NMNH now contains additional examples from Panama and Ecuador. This record marks the southernmost known point in distribution of both the species and genus.

Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar-Cumbray Creek, 25 Jul 1987, L. Reyes A., 1 ♂, 1 ♀; 14 May 1989, 1 ♂; same, but Río Lucumar, El Cholocar, 430 m, 23 Aug 1987, 2 ♂, 1 ♀; same, but Río Lucumar, Simbal, 24 Jun 1988, 1 ♂, 6 ♀; 22 Jul 1989, 2 ♂; 3 Aug 1989, 4 ♀; 15 Apr 1988, 1 ♂; 3 Aug 1988, 4 ♀. Dept. Lambayeque, Río Saña, Saña near the ruins of Corbacho, 30 Sep 1989, 5 ♂, 7 ♀.

Hydroptila constricta Bueno

Hydroptila constricta Bueno, 1984:99.

This species was recently described from Belize, Honduras and Mexico; however, it has more recently been collected in Colombia and Costa Rica. It, too, would appear to have a wide distribution in Central America and northwestern South America. Females associated with males of this species in Colombia are quite different from those recorded as species A and B, below, and agree with the females here recorded.

Material.—Peru, Dept. La Libertad, Prov. Otuzco, Dist. Sinsicap, Río Sinsicap, Sinsicap, 2000 m, 23 Sep 1989, L. Reyes A., 2 ♂, 24 ♀. Dist. Simbal, Río Lucumar, Cumbray, 19 Nov 1988, L. Reyes A., 1 ♂.

Hydroptila ditalea Flint

Hydroptila ditalea Flint, 1968:46.—Bueno, 1984:119.

The species originally was described from the island of Jamaica and subsequently recorded from coastal Mexico. These examples from Peru, and others from Ecuador in the collection of the NMNH, agree with the type and the Mexican examples, except that the twisted tip of the phallic rod differs slightly between the two regions. This tip in the southern region is a bit broader and more sharply angled than the examples from the north where it is quite delicate and strongly curved.

Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 24 Jun 1988, L. Reyes A., 4 ♂, 6 Jul 1989, 4 ♂; 22 Jul 1989, 1 ♂. Dist. Moche, Río Moche at Puente Moche, 3 Jul 1988, 2 ♂; 27 Jul 1988, 7 ♂; 14 Jan 1989, 1 ♂; 18 Jul 1989, 11 ♂; 16 Sep 1989, 15 ♂. Dist. Laredo, Río Moche, Conache, 28 Jul 1989, 3 ♂. Dept. Lambayeque, Río Saña, Saña near the ruins of Corbacho, 30 Sep 1989, 4 ♂.

Hydroptila grenadensis Flint

Hydroptila grenadensis Flint, 1968b:58.

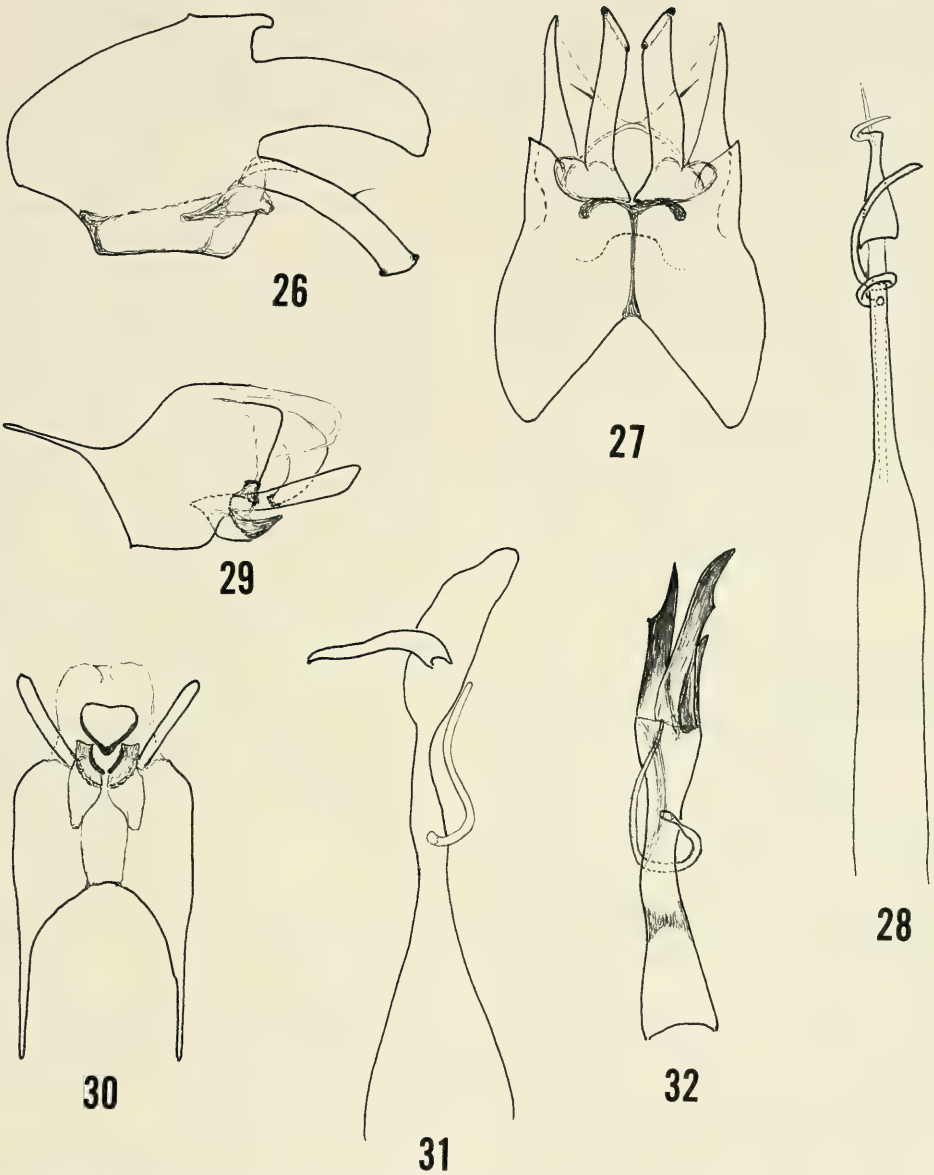
Although this species has only been recorded from the island of Grenada, it is apparently widespread across northern South America and southern Central America. There is material from Trinidad, Colombia, Panama, and Ecuador in the collection of the NMNH.

Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 9 Jul 1988, L. Reyes A., 1 ♂; same, but Río Lucumar-Cumbray Creek, 21 May 1989, 1 ♂. Dept. Lambayeque, Río Saña, Saña, 5 Nov 1989, 1 ♂; same, but near the ruins of Corbacho, 30 Sep 1989, 2 ♂.

Hydroptila sicilicula, new species

Figs. 26–28

This species appears very similar to *H. brailovskyi* Bueno on the basis of the slender claspers and general appearance of the phallus. However, in *H. sicilicula* there is no process posterolaterally from the ninth segment and it is produced apicodorsally, the



Figs. 26–32. Male genitalia of *Hydroptila* and *Neotrichia*. 26–28, *H. sicilicula*: 26, lateral; 27, ventral; 28, phallus. 29–31, *N. riparia*: 29, lateral; 30, ventral; 31, phallus. 32, *N. gotera*, phallus.

tenth tergum is deeply divided mesally and broader and more decurved in lateral aspect, and the claspers end in both dorsal and ventral spots and its tip is slightly rolled laterad. In *H. brailovskyi* the clasper is slightly produced apicodorsally with the only dark spot borne here, and the tip is not rolled laterad.

Adult.—Length of forewing, 2.5 mm. Cleared, in alcohol: pale brown in color. Ninth segment with anterior margin rounded, ventrolateral margin concave; apicodorsally produced into a strong, projecting lobe, semicircular in dorsal aspect; lacking posterolateral spur. Tenth tergum deeply divided dorsomesally, membranous; ventro-

lateral margins lightly sclerotized, broad and slightly decurved in lateral aspect. Subgenital plate rather indistinct in ventral aspect, apparently rounded apically. Clasper in lateral aspect slightly curved, of uniform width, tip slightly rolled laterad with distinct apicodorsal and ventral dark points. Phallus with apical portion less than ¼ length of basal portion; with a well developed spiral process; apical portion inflated basally, tapering apicad, apex twisted into a laterally directed process, central tubule extending slightly beyond process.

Material.—Holotype, male: Peru, Dept. Lambayeque, Río Saña, Saña near the ruins of Corbacho, 30 Sep 1989, L. Reyes A., NMNH. Paratypes: Same data, 4 ♂.

Hydroptila species

Although females were taken with many of the collections of male *Hydroptila ditalea* and *H. grenadensis* as listed above, there is a major problem in the association of the sexes. Females were figured when both of the above species were described; there is no apparent difference in their eighth segments as figured. The same form of female (termed A, below) is common in Peru. There is also a female with a very different eighth segment (termed B). Because there is no way to know which female goes with which species, and that it is possible that both *H. ditalea* and *H. grenadensis* may be mixed under type A and type B may represent yet another species, all females are listed below.

Material.—Type A: Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 24 Jun 1988, L. Reyes A., 1 ♀; 9 Dec 1988, 1 ♀; 6 Jul 1989, 2 ♀; 22 Jul 1989, 4 ♀; same, but Río Lucumar-Cumbray Creek, 19 Nov 1989, 1 ♀. Dist. Moche, Río Moche at Puente Moche, 3 Jul 1988, 3 ♀; 27 Jul 1988, 1 ♀; 14 Jan 1989, 1 ♀; 18 Jul 1989, 5 ♀; 16 Sep 1989, 10 ♀. Dist. Laredo, Río Moche, Conache, 28 Jul 1989, 1 ♀. Dept. Lambayeque, Río Saña, Saña near the ruins of Corbacho, 30 Sep 1989, 7 ♀.

Type B: Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 24 Jun 1988, L. Reyes A., 5 ♀; same, but Río Lucumar-Cumbray Creek, 19 Nov 1989, 2 ♀.

Neotrichia riparia, new species
Figs. 29–31

This distinctive species is a member of the "*Exitrichia*" group of species, similar to as *N. eroga* (Mosely) and, especially, *N. palma* Flint. It differs from other members of the group in lacking any sclerotized dorsolateral projection from the ninth segment and in possessing a decurved, dark-tipped subgenital plate. It is especially similar to *N. palma* in these characteristics, but differs from the latter in having short claspers, in the position of the anterolateral process of the ninth segment, and in having a single spine from the phallus.

Adult.—Length of forewing, 2 mm. Color in alcohol, grayish-brown, wings mottled. Ninth segment with anterolateral process long, slender, at mid-height of segment. Tenth tergum membranous. Subgenital plate developed as a long, dark-tipped, curved process, ending between clasper bases. Bracteole very lightly sclerotized, semierect, parallel-sided. Clasper shorter than bracteole, slightly angled and pointed in lateral aspect, in ventral aspect truncate apically and darkened mesally. Phallus with a spiral process, apex enlarged, with a single large spine which is often everted laterad.

Material.—Holotype, male: Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 24 Jun 1988, L. Reyes A., NMNH. Paratypes: Same data, 3 ♂; same, but 9 Dec 1988, 1 ♂, 4 ♀; same, but 22 Jul 1989, 1 ♂. Dist. Laredo, Río Moche, Conache, 28 Jul 1989, 1 ♂, 3 ♀. Dist. Moche, Río Moche at Puente Moche, 27 Jul 1988, 12 ♂, 12 ♀; 18 Jul 1989, 8 ♂, 15 ♀; 16 Sep 1989, 4 ♂, 2 ♀. Dept. Lambayeque, Río Saña, Saña, 5 Nov 1989, 4 ♂, 20 ♀; same, but near the ruins of Corbacho, 30 Sep 1989, 16 ♂, 12 ♀.

Neotrichia gotera Flint
Fig. 32

Neotrichia gotera Flint, 1983:51.

This species has been known previously only from the unique type from the Province of Salta, in northwestern Argentina. Its discovery in the coastal region of northern Peru represents a major range extension, and suggests that it may be very widespread over the drier areas of western South America.

The genitalia of the two examples are in very good agreement, with some variation. The apicolateral angles of the subgenital plate are drawn-out further in the Peruvian example than in the Argentinian. The major difference is in the spines at the tip of the phallus. The type only has a pair of spines, the Peruvian three (Fig. 32). However, I suspect that the third spine may be broken off the type as it has a large vacant space where the leftmost spine is seen in Fig. 32.

Material.—Peru, Dept. La Libertad, Prov. Otuzco, Dist. Sinsicap, Río Sinsicap, Sinsicap, 2000 m, 23 Sep 1989, L. Reyes A., 1 ♂.

Ochrotrichia (*O.*) *tenanga* Mosely

Polytrichia tenanga Mosely, 1937:185.
Ochrotrichia (*O.*) *tenanga* (Mosely).—Flint, 1972:8; 1981:29.

This is the most widespread Neotropical species of the genus, being recorded from Mexico, Guatemala, Honduras, Costa Rica, Panama, and Venezuela. Nevertheless, its discovery from as far south as northern Peru is somewhat of a surprise.

Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 9 Dec 1988, L. Reyes A., 1 ♂, 2 ♀; 24 Jun 1988, 2 ♂, 5 ♀; 9 Jul 1988, 1 ♂, 1 ♀; 12 Dec 1987, 1 ♀; 6 Jul 1989, 1 ♂, 1 ♀; 5 Sep 1989, 1 ♀. Dist Moche, Río Moche at Puente Moche, 16 Sep 1989, 1 ♂.

Ochrotrichia (*Metrichia*) *malada* Flint

Ochrotrichia (*Metrichia*) *malada* Flint, 1991: 455.

This species, described in a paper on the Trichoptera of the Department of Antioquia, Colombia, is here recorded from Peru. There is close agreement between the type and this example in the structures of the abdomen, but a number of small differences in the genitalia. In the Peruvian example the apicoventral angle of the clasper protrudes slightly, rather than recedes, and the dorsolateral hook is shorter and not bent laterad subapically.

Material.—Peru, Dept. La Libertad, Prov. Otuzco, Dist. Sinsicap, Río Sinsicap, Sinsicap, 2000 m, 23 Sep 1989, L. Reyes A., 1 ♂.

Oxyethira parce (Edwards & Arnold)

Protoptila parce Edwards & Arnold, 1961: 405.—Edwards, 1973:496.

This species was erroneously synonymized by Flint (1981) with *Oxyethira azteca* (Mosely). During the preparation of this paper it was discovered that two very closely related species have been confused under the name of *O. azteca.* What is judged to be the true *O. azteca,* based on the original excellent illustrations of Mosely, is not as widely distributed as the closely related *O. parce,* although both have exceedingly wide distributions. Several collections from Venezuela and Colombia even contain the two species taken together.

Figures (33–43) showing the differences in the male and female genitalia of the two species are given here. In the male the differences are to be most clearly seen in the complex of ninth segment-inferior appendages-subgenital plate-bilobed process. In *O. azteca* in lateral aspect (Fig. 33) the dorsal process of ninth segment-inferior appendages lobe is almost at midlength, whereas in *O. parce* it is barely more than a third of

the length of the lobe (Fig. 39); the bilobed process is more strongly arched and much shorter in *O. azteca* than in *O. parce* in which the bilobed process is longer and more closely appressed to the dorsolateral margins of the subgenital plate. In dorsal aspect (Fig. 41) the basalmost extension of the bilobed process in *O. parce* reaches a bit more than half the distance from the dorsal process to the base of the ninth segment whereas in *O. azteca* it extends only about one-third of this distance (Fig. 36). The apicoventral lip of the phallus in *O. parce* is much longer than in *O. azteca* (Figs. 40 and 34). In the female vaginal sclerites there is, in *O. parce,* an erect process at the base of the lightly sclerotized basal sac (Fig. 42) which is lacking in *O. azteca* (Fig. 37). The latter has a decumbent lobe arising more apicad which might be confused with these processes. There are other differences in the vaginal sclerites, but their appearance varies very strongly with the degree of pigmentation of the parts.

Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 12 Dec 1987, L. Reyes A., 2 ♂; 24 Jun 1988, 1 ♀; 9 July 1988, 1 ♂; same, but Río Lucumar-Cumbray Creek, 19 Nov 1988, 1 ♂, 2 ♀. Dist. Moche, Río Moche at Puente Moche, 14 Jan 1989, 2 ♂; 18 Jul 1989, 12 ♂, 4 ♀; 16 Sep 1989, 19 ♂, 11 ♀.

Family Leptoceridae

Nectopsyche spiloma (Ross)

Leptocella spiloma Ross, 1944:219.
Nectopsyche spiloma (Ross).—Haddock, 1977:392.

This species was originally described from Kansas in the United States, but subsequently recorded from Guatemala, Honduras, Mexico, Nicaragua and Panama. Additional material has been seen from Costa Rica and Ecuador, and now its presence in northern Peru is noted. This range is almost as great as than of *N. punctata,* listed below, but extends more to the north than does *N. punctata* which is much more widespread in South America.

Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Simbal (village), 15 Apr 1988, L. Reyes A., 2 ♂; same, but Río Lucumar, Simbal, 24 Jun 1988, 3 ♀; same, but Río Lucumar-Cumbray Creek, 12 May 1987, 1 ♂; 25 Jul 1987, 1 ♂; 12 May 1989, 1 ♂; 21 May 1989, 3 ♂; same, but Río Lucumar, Cholocar, 17 Sep 1989, 2 ♂. Dist. Laredo, Río Moche, Conache, 28 Jul 1989, 7 ♂. Dist. Moche, Río Moche at Puente Moche, 27 Jun 1988, 1 ♂, 3 ♀; 16 Sep 1989, 5 ♂, 2 ♀.

Nectopsyche punctata (Ulmer)

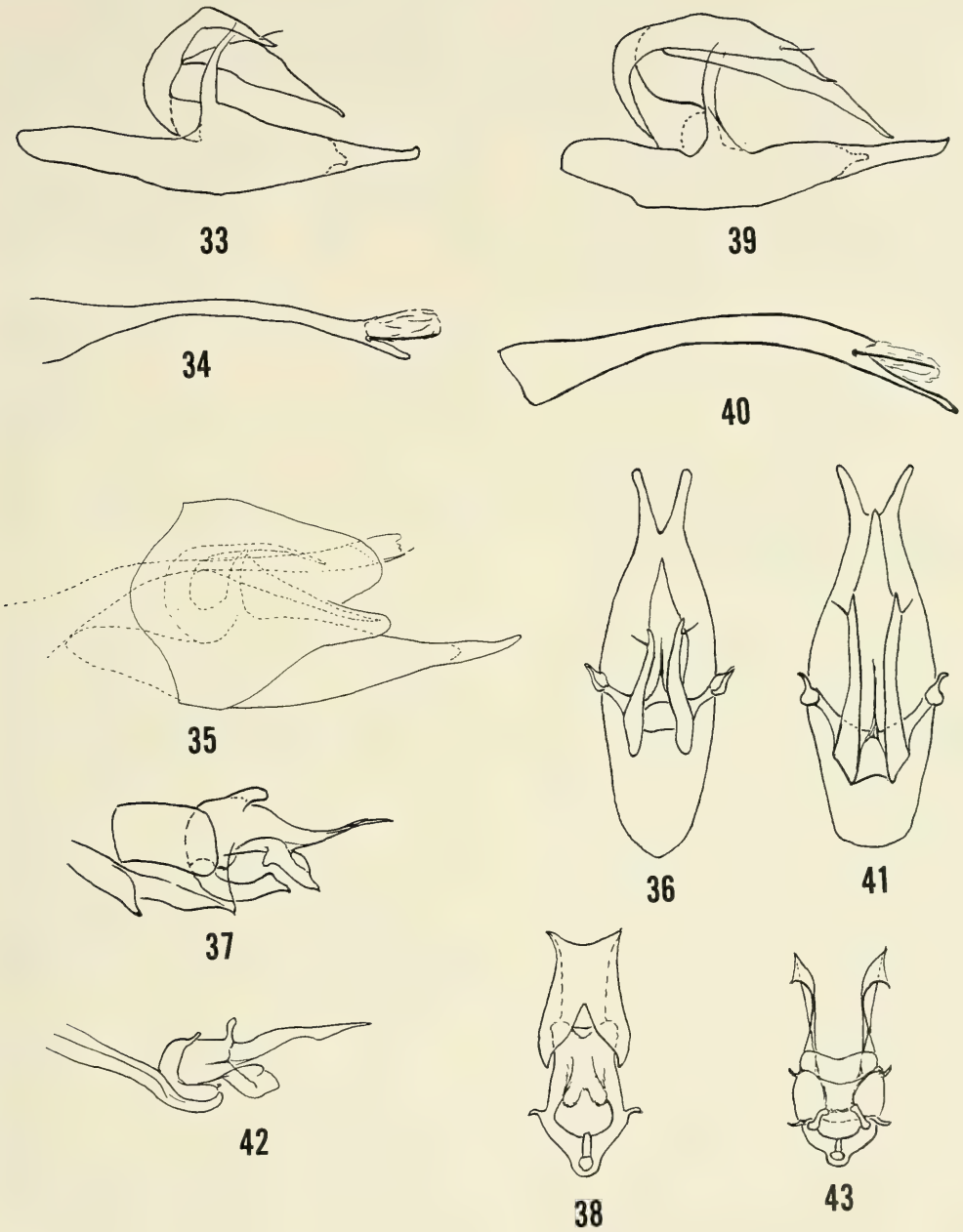
Leptocella punctata Ulmer, 1905:75.—Fischer, 1966:60.
Nectopsyche punctata (Ulmer).—Flint, 1981: 34.

This species is very widely distributed in the neotropics, being known from central Mexico south to central Argentina, in both lowland and upland areas. The color pattern on the wings varies considerably in different areas, resulting in considerable synonymy (Fischer 1966, Flint 1981). The species apparently has not been recorded from Peru before, although material from the Departments of Cusco, Huanuco, Junín, Lima, Loreto, Madre de Dios and Pasco has been seen by Flint.

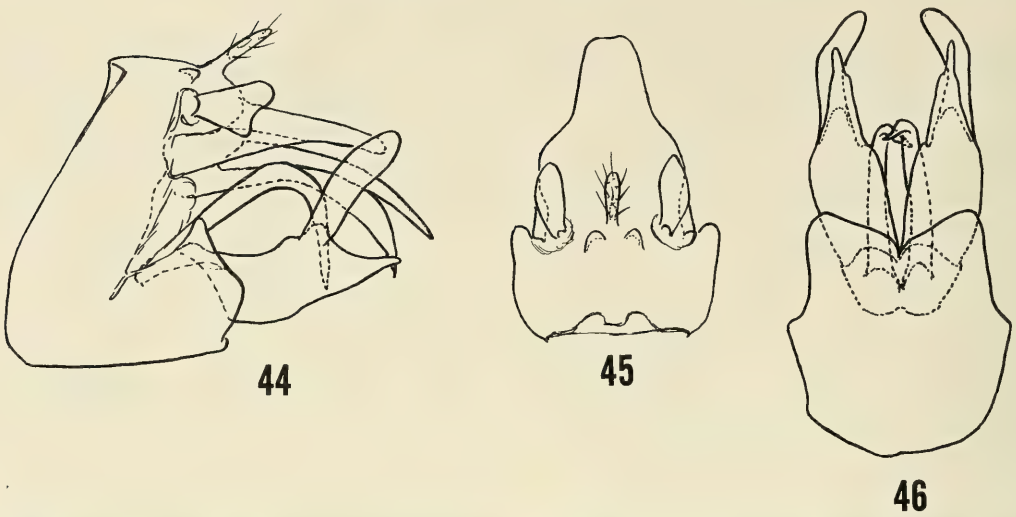
Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Moche, Río Moche at Puente Moche, 27 Jun 1988, Luis Gil, 1 ♂; same, but 16 Sep 1989, L. Reyes A., 6 ♂. Dept. Lambayeque, Río Saña, Oyotún, 200 m, 18 Nov 1989, 1 ♂, 1 ♀.

Triaenodes peruanus, new species
Figs. 44–46

Although three species of *Triaenodes* have been described from the neotropics, *T. columbica* Ulmer is totally unlike the other known Neotropical species and its genitalia



Figs. 33–43. Genitalia of *Oxyethira*. 33–38, *O. azteca*: 33, male ninth segment and beyond, lateral; 34, phallus, lateral; 35, male genitalia, lateral; 36, male ninth segment and beyond dorsal; 37, female vaginal sclerites, lateral; 38, same, dorsal. 39–43, *O. parce*: 39, male ninth segment and beyond, lateral; 40, phallus, lateral; 41, male ninth segment and beyond, dorsal; 42, female vaginal sclerites, lateral; 43, same, dorsal.



Figs. 44–46. Male genitalia of *Triaenodes peruanus*: 44, lateral; 45, ninth and tenth terga and cerci, dorsal; 46, ninth sternum and claspers, ventral.

seem more similar to certain African groups (K. Manuel, pers. comm.) suggesting a mislabeled type. The Costa Rican species, *T. delicatus* Navas, is quite similar to *T. peruanus* in its genitalia and coloration. However, in *T. delicatus* the mid-dorsal process of the ninth tergum is longer, the cercus is barely widened apicad, the apex of the tenth tergum is drawn out into a narrow point, and the phallic parameres are longer with a lateral point at midlength.

Adult.—Length of forewing, male 4.5–5 mm, female 5.5–7 mm. Color overall tawny, immaculate; appendages, head and thorax dorsally paler; forewing tawny. Male genitalia: Ninth segment slightly expanded anteroventrally, with an erect middorsal process and low dorsolateral knobs. Cercus short, expanded apicad, apical margin slightly bilobate in lateral aspect. Tenth tergum elongate, tapered apicad, apex rounded. Clasper with a basodorsal process whose apical half is sharply angled ventrad; with a thin, pale dorsolateral lobe of uniform width; apical lobe tapering to a point. Phallus with a long mesoventral sclerite and paired dorsolateral parameres of same length as mesoventral sclerite.

Material.—Holotype, male: Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 9 Jul 1988, L. Reyes A., NMNH. Paratypes: Same data, 1 ♂, 4 ♀; same, but 3 Aug 1988, 2 ♀; same, but 24 Jun 1988, 1 ♂, 1 ♀; same, but 5 Sep 1989, 1 ♂.

Family Helicopsychidae
Helicopsyche vergelana Ross

Helicopsyche vergelana Ross, 1956:440.—Flint, 1981:37.

This species is widely distributed in the northern neotropics: Mexico through Central America, east to Suriname, and now south to northern Peru.

Material.—Peru, Dept. La Libertad, Prov. Trujillo, Dist. Simbal, Río Lucumar, Simbal, 12 Dec 1987, L. Reyes A., 6 ♂, 1 ♀; 12 Oct 1987, 3 ♂; same, but Río Lucumar-Cumbray Creek, 25 Jul 1987, 2 ♂, 2 ♀; 27 Jun 1988, 3 ♂, 1 ♀.

Acknowledgments

The authors express their appreciation to: Dr. P. O. Whalley of the British Museum

(Natural History) for the loan of the type of *Smicridea saucia* McLachlan; Mr. Young T. Sohn, Scientific Illustrator of the Department of Entomology, Smithsonian Institution, for the preparation of Fig. 7; and to the reviewers of this article for their very valuable criticisms.

Postscript

Shortly after Flint received the corrected copy of the major part of this manuscript from Reyes, he received notice that Biologo Luis Reyes Arrunategui died on April 18, 1990, in a traffic accident on his way to collect in the field. Reyes had just started a survey of the the Río Saña, Department of Lambayeque for his thesis to obtain the Bachelor of Biological Science degree. His first collection from this Río had been sent to Flint and the results of their study have been incorporated into this work as they add further insight into the caddisfly fauna of this poorly known region of the world.

The death of Lucho is a great shock to me. He was the most promising young man to begin the study of caddisflies in South America. Although greatly hampered by the lack of library and reference collection, he was an indefatigable collector and an avid student of these insects. I count myself lucky to have had a month in the field with him on the Biolat expedition to Pakitza in September of 1988.

Literature Cited

Anonymous. 1973. Inventario, evaluacion y uso racional de los recursos naturales de la costa. Cuenca del Río Moche.—Oficina Nacional de Evaluacion de Recursos Naturales, Lima, Peru, Volumes I and II.

———. 1987. Peru: caracteristicas geograficas a nivel distrital: superficie–densidad–cartografia.—Boletin de Estadisticas Geograficas No. 1, 437 pp.

Banks, N. 1910. New South American neuropteroid insects.—Proceedings of the Entomological Society of Washington 12:146–160.

Bueno-Soria, Joaquin. 1984. Estudios en insectos acuaticos II. Revision para México y Centroamérica del género *Hydroptila* Dalman, 1819 (Trichoptera Hydroptilidae).—Folia Entomologica Méxicana 59:79–138.

Edwards, Sidney W. 1973. Texas caddisflies.—The Texas Journal of Science 24:491–516.

———, & Connie R. Arnold. 1961. The caddis flies of the San Marcos River.—The Texas Journal of Science 13:398–415.

Fischer, F. C. J. 1962. Polycentropodidae, Psychomyiidae.—Trichopterorum Catalogus 3:1–236.

———. 1963. Hydropsychidae, Arctopsychidae.—Trichopterorum Catalogus 4:1–223.

———. 1966. Leptoceridae, Pars 2.—Trichopterorum Catalogus 7:1–163.

———. 1972. Supplement to volumes III and IV.—Trichopterorum Catalogus 13:1–172.

Flint, Oliver S., Jr. 1963. Studies of neotropical caddis flies, I: Rhyacophilidae and Glossosomatidae (Trichoptera).—Proceedings of the United States National Museum 114(3473):453–478.

———. 1967. Studies of neotropical caddis flies, V: Types of the species described by Banks and Hagen.—Proceedings of the United States National Museum 123(3619):1–37.

———. 1968a. The caddisflies of Jamaica (Trichoptera).—Bulletin of the Institute of Jamaica, Science Series 19:1–68.

———. 1968b. Bredin-Archbold-Smithsonian Biological Survey of Dominica 9. The Trichoptera (Caddisflies) of the Lesser Antilles.—Proceedings of the United States National Museum 125(3665):1–86.

———. 1970. Studies of neotropical caddisflies, X: *Leucotrichia* and related genera from North and Central America (Trichoptera: Hydroptilidae).—Smithsonian Contributions to Zoology 60:1–64.

———. 1972. Studies of neotropical caddisflies, XIII: The Genus *Ochrotrichia* from Mexico and Central America (Trichoptera: Hydroptilidae).—Smithsonian Contributions to Zoology 118:1–28.

———. 1974a. Studies of neotropical caddisflies, XVIII: New species of Rhyacophilidae and Glossosomatidae (Trichoptera).—Smithsonian Contributions to Zoology 169:1–30.

———. 1974b. Studies of neotropical caddisflies, XVII: The genus *Smicridea* from North and Central America (Trichoptera: Hydropsychidae).—Smithsonian Contributions to Zoology 167:1–65.

———. 1975. Studies of neotropical caddisflies, XX: Trichoptera collected by the Hamburg South-Peruvian expedition.—Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg 4(90):565–573.

———. 1980. Results of the Catherwood Bolivian-Peruvian Altiplano Expedition. Part I, aquatic

insects except Diptera: VI. Trichoptera.—Proceedings of the Academy of Natural Sciences of Philadelphia 132:213–217.

———. 1981. Studies of neotropical caddisflies, XXVIII: The Trichoptera of the Río Limon basin, Venezuela.—Smithsonian Contributions to Zoology 330:1–61.

———. 1983. Studies of neotropical caddisflies, XXXIII: New species from Austral South America (Trichoptera).—Smithsonian Contributions to Zoology 377:1–100.

———. 1988. Studies of neotropical caddisflies, XXXIX: The genus *Smicridea* in the Chilean subregion (Trichoptera: Hydropsychidae).—Smithsonian Contributions to Zoology 472:1–45.

———. 1991. Studies of neotropical caddisflies, XLV: The taxonomy, phenology, and faunistics of the Trichoptera of Antioquia, Colombia.—Smithsonian Contributions to Zoology 520:1–113.

Haddock, J. D. 1977. The biosystematics of the caddis fly genus *Nectopsyche* in North America with emphasis on the aquatic stages.—The American Midland Naturalist 98:382–421.

Kimmins, D. E. 1957. Lectotypes of Trichoptera from the McLachlan collection now in the British Museum (Natural History).—Bulletin of the British Museum (Natural History), Entomology 6(4):91–126.

Maes, Jean-Michel, & Oliver S. Flint, Jr. 1988. Catálogo de los Trichoptera de Nicaragua.—Revista Nicaraguense de Entomologia 2:1–11.

Martynov, A. B. 1912. On two collections of Trichoptera from Peru.—Annuaire de Musée zoologique de l'Académie Impériale des Sciences de St. Pétersbourg 17:1–40.

McLachlan, Robert. 1871. On new forms, etc., of extra-European trichopterous insects.—Journal of the Linnean Society of London, Zoology 11: 98–141.

Mosely, Martin E. 1937. Mexican Hydroptilidae (Trichoptera).—The Transactions of the Royal Entomological Society of London 86:151–190.

———. 1954. The *Protoptila* group of the Glossosomatinae (Trichoptera: Rhyacophilidae).—Bulletin of the British Museum (Natural History), Entomology 3(9):317–346.

Navas, L. 1923. Estudis sobre neuropters (Insectes).—Arxius de l'Institut de Ciencies 7:179–203.

Roback, Selwyn S. 1966. The Catherwood Foundation Peruvian-Amazonian Expedition. XI-The Trichoptera larvae and pupae.—Monographs of the Academy of Natural Sciences of Philadelphia 14:235–303.

Ross, Herbert H. 1944. The caddis flies, or Trichoptera, of Illinois.—Illinois Natural History Survey Bulletin 23(1): 1–326.

———. 1956. New species of *Helicopsyche* from the Western Hemisphere (Trichoptera: Helicopsychidae).—Journal of the Washington Academy of Sciences 46:397–401.

———. 1959. New species of *Chimarra* from Mexico and Central America (Trichoptera, Philopotamidae).—Entomological News 70:169–178.

Tosi, Joseph A. 1960. Zonas de vida natural en el Peru; memoria explicativa sobre el mapa ecologico del Peru.—Instituto Interamericano de Ciencias Agricolas de la OEA, zona Andina, Proyecto 39, Programa de Cooperation Technica, Boletin Technico No. 5, 271 pp.

Ulmer, Georg. 1905. Neue und weinig bekannte aussereuropaischer Trichopteren, hauptsachlich aus dem Wiener Museum.—Annalen des kaiserlich-koniglichen naturhistorischen Hofmuseums 20: 59–98.

———. 1909. Argentinische Trichopteren.—Zeitschrift fur wissenschaftliche Insektenbiologie 5: 73–76.

Weidner, H. 1964. Die Entomologischen Sammlungen des Zoologischen Staatsinstituts und Zoologischen Museums Hamburg, X. Teil, Insecta VII.—Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut 62:55–100.

(OSF) Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 493–537

AN EXAMINATION OF THE SHRIMP FAMILY CALLIANIDEIDAE (CRUSTACEA: DECAPODA: THALASSINIDEA)

Brian Kensley and Richard W. Heard

Abstract.—One striking character was found to unite the members of the family Callianideidae, viz. the presence of rows of plumose setae, each seta sited in a pit, these rows being found on the carapace, abdominal pleura, and propodi of pereopods 2–4. Several new taxa are described: *Crosniera,* new genus (for *Callianassa minima* Rathbun, 1901); *Michelea,* new genus (for *Callianidea vandoverae* Gore, 1987, *Callianidea leura* Poore & Griffin, 1979, *Callianidea lepta* Sakai, 1987, plus the new species *M. pillsburyi* and *M. lamellosa*); *Mictaxius,* new genus (with the new species *M. thalassicola*); *Marcusiaxius lemoscastroi* Rodrigues & Carvalho, 1972, is redescribed, along with *M. colpos,* new species, while six species of *Meticonaxius* are discussed, with *Meticonaxius bouvieri,* new species described. A cladistic analysis of 11 taxa suggested that, within the Callianideidae, pleopodal respiratory filaments arose twice, that the linea thalassinica and the dentate ischial crest of maxilliped 3 have twice been lost, and that the *Thomassinia-Crosniera-Mictaxius* group of genera are most closely related to the Callianassidae.

In the continuing effort to bring clarity to the systematics of the thalassinidean decapods, individual genera and families are being examined in detail (e.g., Kensley 1989, Kensley & Heard 1990). Morphological characters in particular are being reassessed, in an attempt to establish relationships. With this objective in view, the western Atlantic members of the Callianideidae possessing accessory respiratory filaments of the pleopods were examined, but it became apparent that several thalassinidean species lacking these filaments should also be included in this group; the review was thus expanded beyond the western Atlantic. Of the group possessing respiratory filaments on the pleopods, the genus *Callianidea* is diagnosed, a new genus *Michelea* created to accommodate *Callianidea vandoverae,* two Pacific species, and two new species. In the group lacking pleopodal filaments, the species of the genera *Meticonaxius* and *Marcusiaxius* are reviewed or redescribed, and one new species of each described; the genus *Thomassinia* is examined, along with the seemingly closely-related '*Callianassa*' *minima* and the new genus *Mictaxius.*

For comparative purposes, material of the Pacific *Callianidea typa* H. Milne Edwards, 1837, was examined from Bikini Atoll, Saipan, Guam, and Tahiti, as was the holotype of *Callianidea lepta* Sakai, 1987, from Japan (USNM 231419).

Common to all these forms is the presence of short plumose setae, each seta sited in a pit-like structire, these pits usually arranged in tight rows. From hereon referred to, for the sake of brevity, as 'setal rows,' these rows are found on the anterolateral carapace, on the pleural region of each abdominal somite, and on the propodi of pereopods 2–4 (Fig. 1). Amongst the callianideid genera, the arrangement and siting of these setal rows fall into three patterns, illustrated in Fig. 2.

The number and position of exopods and

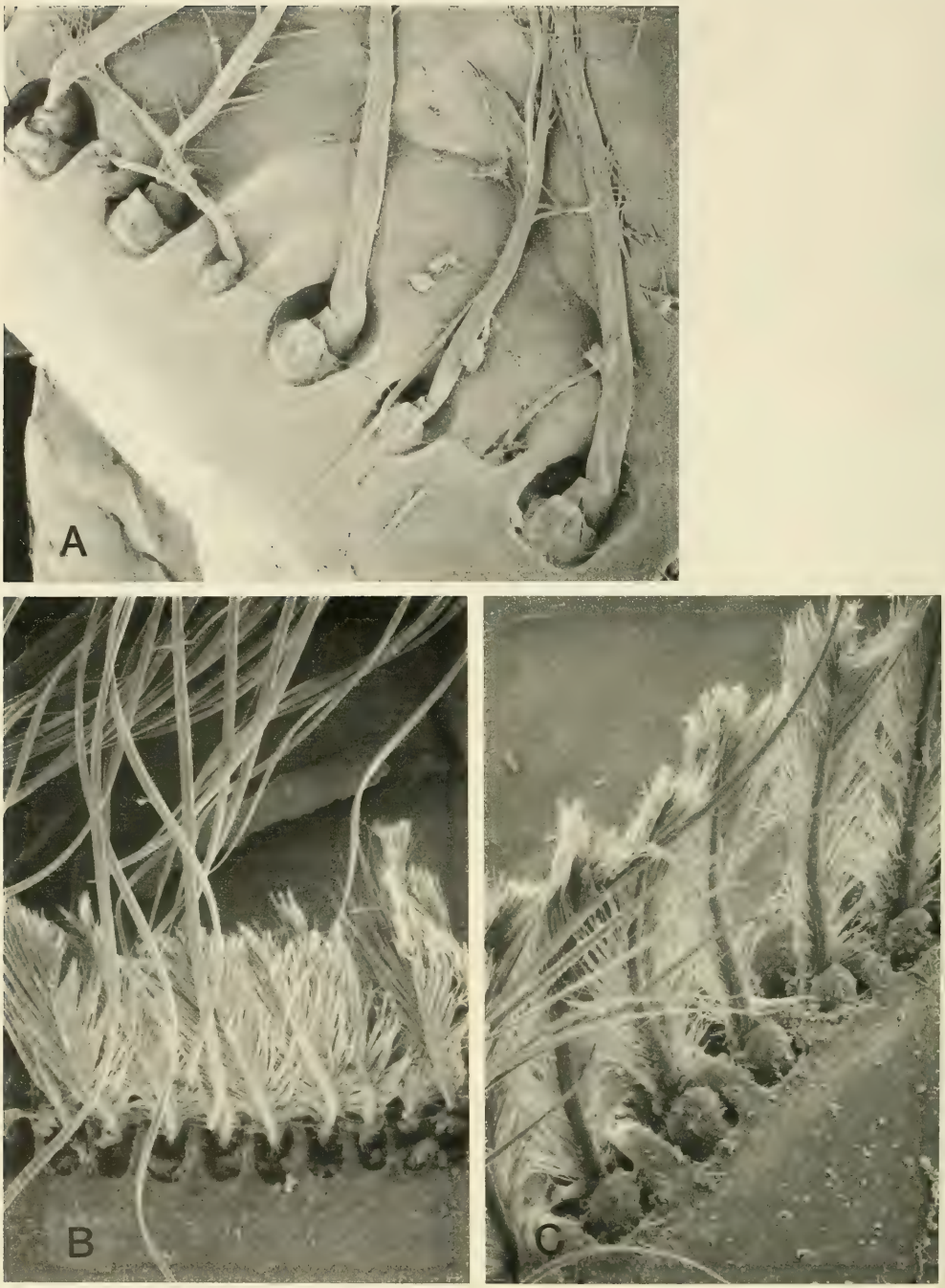


Fig. 1. SEM micrographs of *Marcusiaxius colpos*: A, Setal row from pleuron 2, 350×; B, Setal row from propodus of pereopod 3, 150×; C, Setal row from propodus of pereopod 3, 250×.

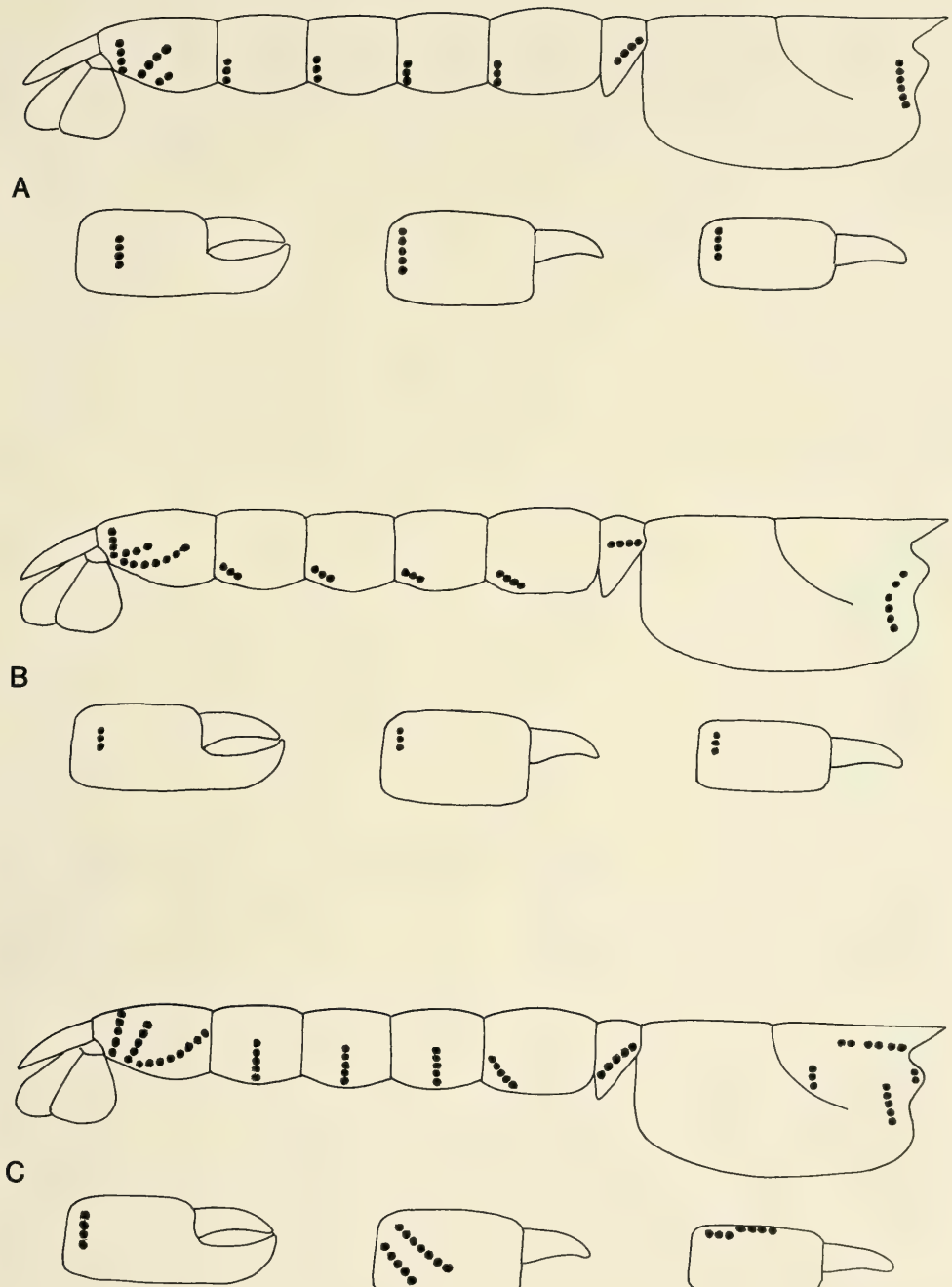


Fig. 2. Diagrammatic representation of three patterns of setal row distribution on carapace and abdomen (above) and propodi of pereopods 2–4 (below): A, *Callianidea* (pattern 0); B, *Crosniera* (pattern 1); C, *Marcusiaxius* (pattern 2).

Table 1.—Distribution of exopods, epipods, and gills.

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
A. *Callianidea laevicauda*								
Exopod	1	1	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	—	—	—	—	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
B. *Crosniera minima*								
Exopod	1	1	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	r	r	r	r	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
C. *Marcusiaxius colpos*								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	1	1	1	1	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	1	1	1	—
D. *Marcusiaxius lemoscastroi*								
Exopod	1	1	—	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	1	1	1	1	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	1	1	1	—
E. *Meticonaxius bouvieri*								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	1	1	1	1	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	1	1	1	—
F. *Meticonaxius longispina*								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	r	r	r	r	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	1	1	1	—
G. *Meticonaxius microps*								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	1	1	1	1	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
H. *Meticonaxius monodon*								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	1	1	1	1	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	1	1	1	—

Table 1.—Continued.

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
I. *Michelea lamellosa*								
Exopod	1	r	1	—	—	—	—	—
Epipod	1	1	1	—	—	—	—	—
Podobranch	—	—	—	—	—	—	—	—
Arthrobranch	—	—	r + r	r + r	r + r	r + r	r	—
Pleurobranch	—	—	—	—	—	—	—	—
J. *Michelea pillsburyi*								
Exopod	1	r	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	—	—	—	—	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
K. *Michelea vandoverae*								
Exopod	1	1	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	r	r	r	r	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	r	—
L. *Mictaxius thalassicola*								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	r	—
Podobranch	—	—	r	r	r	r	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—

gills for each species (wherever possible) are presented in Table 1. In these tables, 'r' implies rudimentary or reduced.

Abbreviations: BLM = Bureau of Land Management; MAFLA = Mississippi-Alabama-Florida BLM Program; MCZ = Museum of Comparative Zoology, Harvard University; RMNH = Rijksmuseum van Natuurlijke Historie, Amsterdam; SAM = South African Museum, Cape Town; USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZMC = Zoological Museum, University of Copenhagen; ovig. = ovigerous.

In the following systematic section, genera, and species within genera, are arranged alphabetically.

Family Callianideidae Kossmann, 1880

Callianideidae Kossmann, 1880:80.—Gurney, 1938:343.—de Saint Laurent, 1979: 1395.—Poore & Griffin, 1979:221.

Callianideinae De Man, 1928:30.—Melin, 1939:4.—Balss, 1957:1582.—de Saint Laurent, 1973:515.—Sakai & Holthuis, 1987:94.—International Commission on Zoological Nomenclature, 1989:61.

Diagnosis.—Gonochoristic. Carapace somewhat compressed; rostrum short or reduced, lacking spines or teeth, or with few low teeth; cervical groove well developed to obsolete; linea thalassinica complete (i.e., reaching posterior margin of carapace), incomplete, or lacking; anterior region bearing 1 to 4 rows of specialized setae and pits. Abdominal pleura, especially of somite 1, poorly developed, with or lacking lateral anterodorsal lobe for articulation-locking with posterior carapace; 1 or more rows of setal pits present on abdominal somites. Scaphognathite of maxilla 2 with single elongate spinulose 'whip' seta reaching posteriorly into branchial chamber (very rarely, 2 elongate whips present). Maxilliped 2, ex-

opod well developed or reduced. Maxilliped 3 pediform, becoming somewhat broadened in some forms; dentate ischial crest present or absent. Pereopod 1, chelipeds subsimilar and subequal in size, or markedly different. Pereopod 2 chelate. Propodi of pereopods 2, 3, and 4 expanded in some species, bearing 1 or more rows of setal pits on lateral surface. Epipods present on pereopods 1–4 in all but one species. Pleopod 1 of female uniramous, of 2 articles. Pleopod 1 of male uniramous, of 2 articles, reaching anteriorly to thoracic sternites. Pleopod 2 of male bearing rod-shaped appendix masculina. Pleopods 2–5, rami variously fringed with filaments or lamellae (these presumed to have a supplemental respiratory function), or becoming broad, expanded and lacking respiratory filaments; appendix interna present, free in most species. Uropodal rami lacking transverse suture, lateral ramus bilobed in one species. Telson lacking non-articulating dorsal or lateral spines.

Key to the Genera of Callianideidae

1. Respiratory filaments present on pleopods 2
– Respiratory filaments lacking on pleopods 3
2. Pereopod 1, chelipeds strikingly dissimilar ..... *Callianidea*
– Pereopod 1, chelipeds subsimilar ..... *Michelea*
3. Linea thalassinica present 4
– Linea thalassinica absent 6
4. Linea thalassinica reaching posterior margin of carapace .....*Mictaxius*
– Linea thalassinica not reaching posterior margin of carapace 5
5. Maxilliped 3, exopod lacking; Ischium lacking dentate crest .... *Thomassinia*
– Maxilliped 3, exopod present; Ischium having dentate crest . . *Crosniera*
6. Maxilliped 3 lacking dentate ischial crest; Rostrum having submarginal dense pile of setae ..... *Marcusiaxius*
– Maxilliped 3 having dentate ischial crest; Rostrum lacking dense pile of setae ..... *Meticonaxius*

Callianidea H. Milne Edwards, 1837

Callianidea H. Milne Edwards, 1837:319.—Boas, 1880:108, 110.—Bate, 1888:10.—Rathbun, 1901:94.—Borradaile, 1903: 548.—Gurney, 1938:301, 342.—Balss, 1957:1582.—Melin, 1939:4.—de Saint Laurent, 1973:515.—Le Loeuff & Intes, 1974:23.—Sakai & Holthuis, 1987:93.—International Commission of Zoological Nomenclature, 1989:61.

Type species.—By monotypy, *Callianidea typa* H. Milne Edwards, 1837.

Gender.—Feminine.

Diagnosis.—Carapace lacking linea thalassinica, or with very short anterior linea thalassinica. Anterolateral carapace with vertical row of setae in postantennal area. Abdominal somite 1 with small anterodorsal rounded sclerotized articulating plate, separated by non-sclerotized integument from larger sclerotized posterior plate; latter tapering ventrally but with no free pleuron, with irregular oblique setal row. Somite 2–5 each having short row of few setae in posteroventral angle of pleuron; somite 6 with 3 poorly defined irregular setal rows. Antennular peduncle with article 1 not elongate, article 3 about 1/7 carapace length. Article 4 of antennal peduncle about 1/4 carapace length. Antennal acicle reduced to tiny scale. Lateral epistome bearing cluster of elongate setae. Mandibular incisor having 7 rounded teeth. Maxilliped 2 with well developed exopod. Maxilliped 3 with dentate ischial crest. Pereopod 1, chelipeds highly unequal, similar in ♂ and ♀. Pereopods 2–4, propodus with short vertical setal row proximally on lateral surface. Pleurobranchs lacking. Pleopodal branchial filaments of 2 to 4 articles, borne on mesial and lateral margins of both rami.

Callianidea laevicauda Gill, 1859
Figs. 3, 4, Table 1A

Callianidea laevicauda Gill, 1859:167.—Rathbun, 1901:94.—De Man, 1928:21.—Schmitt, 1924:79; 1935:193, fig. 54; 1936: 375.—Rodrigues, 1983:93.

Callianidea laevicauda occidentalis Schmitt, 1939:10.

Callianidea Steenstrupii Boas, 1880:108 [188].

Material examined.—USNM 24663, ♀ cl 14.7 mm, Ensenada Honda, Culebra, Puerto Rico.—USNM 47359, ♀ cl 5.9 mm, Jamaica.—USNM 57514, ♀ cl 8.9 mm, Caracas Bay, Curaçao, under intertidal stones.—USNM 57924, ovig. ♀ cl 11.0 mm, Needham's Point, Barbados.—USNM 67422, ♀ cl 5.1 mm, Kralendijk, Bonaire, under intertidal stones.—USNM 68713, ovig. ♀ cl 10.3 mm, ♀ cl 11.1 mm, Needham's Point, Barbados.—USNM 68722, ♀ cl 11.9 mm, Pelican Is., Barbados.—USNM 122446, ovig. ♀ cl 10.2 mm, Grande Bay, St. Maarten, intertidal.—USNM 221759, ♂ cl 6.3 mm, San Salvador Is., Bahamas, intertidal pool.—USNM 221760, ♀ cl 8.0 mm, Carrie Bow Cay, Belize, back-reef rubble, 1 m.—USNM 243465, 3 ♂ cl 6.6 mm, 7.2 mm, 11.3 mm, 3 ♀ cl 6.0 mm, 8.8 mm, 8.8 mm, Caledonia Bay, Atlantic Panama, intertidal.—USNM 243466, 5 ♂ cl 5.4 mm, 7.2 mm, 8.5 mm, 9.4 mm, 10.0 mm, 3 ♀ cl 5.4 mm, 9.6 mm, 11.5 mm, Smithsonian-Bredin Freelance Expedition sta 73-56, English Harbour, Antigua.—USNM 243467, ovig. ♀ cl 14.2 mm, 3 ♀ cl 6.5 mm, 7.7 mm, 14.0 mm, Smithsonian-Bredin Freelance Expedition sta 21-56, Baradal, Tobago Cays, Grenadines, under intertidal rocks.—ZMC, ♂ cl 12.3 mm, 5 +, cl 4.2 mm, 8.8 mm, 11.1 mm, 12.0 mm, 13.2 mm, Tobago, coll. Dr. Th. Mortensen Expedition 1914-1916.—ZMC, ♀ cl 11.4 mm, St. Johns, U.S. Virgin Islands.—Syntype of *Callianidea steenstrupii* Boas, ZMC, ♀ cl 10.4 mm, Barbados, coll. 1866.

Description.—Carapace with cervical groove in posterior half, reaching dorsal midline. Rostrum barely demarked, low, apically broadly rounded. Linea thalassinica very short, extending posteriorly from orbit. Irregular vertical row of setal pits in postantennal-postepistomal region.

Eye with cornea demarked, situated laterally at about midlength of eyestalk, mediodistal portion of stalk flattened. Antennular peduncle reaching distal third of antennal peduncle article 4, with articles increasing in length distally, none markedly elongate. Antennal peduncle with acicle reduced to tiny rounded plate, article 4 slender, elongate, article 5 slightly more than half length of article 4. Lateral epistome with band of elongate setae reaching anteriorly almost to distal end of antennular peduncle. Mandible with incisor having 7 blunt teeth, molar broadly rounded with few mesial tubercles; palp of 3 articles, distal article longest, heavily setose. Remainder of mouthparts as figured. Maxilliped 1, endopod with slender digitiform distal article. Maxilliped 2, exopod well developed, with distal segmented flagellum. Maxilliped 3, merus with low blunt spine distally on posterior margin. Pereopod 1, chelipeds strongly dissimilar; larger cheliped with ischium having serrate posterior margin, merus with 2 or 3 low tubercles on posterior margin, chela robust, propodal palm twice length of fingers, propodal carina along posterior margin obscurely crenulate, ridge on mesial face of fixed finger entire, cutting edge with 3 rounded proximal tubercles and strong triangular tooth at about midlength; dactylus strongly curved, cutting edge with strong truncate tubercle proximally, well separated from triangular tooth. Smaller cheliped slender, ischium and merus unarmed; carpus of similar width and about ⅔ length of propodal palm, latter about 2½ times length of fingers, fixed finger with several triangular teeth distally on cutting edge, dactylar cutting edge entire. Pereopod 2, cutting edges of chela bearing fine spines; propodus with short proximal setal row on lateral surface.

Pereopod 3 almost subchelate, propodus broad, flattened, about ⅓ longer than wide, with short proximal setal row on lateral surface, posterodistal angle somewhat produced, bearing stout spine. Pereopod 4, propodus with strong posterodistal spine, 2 short setal rows proximally on lateral surface; dactylus somewhat twisted. Pereopod 5, dactylus twisted.

Pleopod 1 in female of 2 articles, distal article slender-lanceolate. Pleopod 1 in male of 2 articles, distal article broadly triangular, with small mesial lobe bearing hooks. Pleopod 2 in male with rod-shaped setose appendix masculina and short free appendix interna. Pleopods 2–5 with both rami bearing marginal slender cylindrical accessory respiratory filaments, each filament proximally of 2 articles, more distal filaments of up to 4 articles. Abdominal somite 6 with 1 vertical row and 2 irregular oblique rows of setal pits posterolaterally, plus short submarginal row near posterolateral angle. Uropod with outer ramus having small basal spine on dorsal surface, margin setose with additional row of small golden spines along most of laterodistal margin; inner ramus with longitudinal dorsal ridge bearing 2 spines in distal half. Telson slightly longer than greatest width, posterior margin subtruncate, setose.

Remarks.—Schmitt (1939) described the new subspecies *Callianidea laevicauda occidentalis,* from Socorro Island (Pacific Mexico) and the Galapagos Islands. In the description, he noted that the only differences from the Atlantic *C. laevicauda* were the somewhat more tuberculate lower propodal carina, and the crenulate mesial ridge of the fixed finger of the larger first pereopod chela. Examination of material from the Galapagos, Lower California, and Pacific Mexico confirmed Schmitt's observations, but revealed some variation in these characters. Separation of Pacific and Atlantic forms of this species is thus based on very thin evidence. Given the wide distribution across the Caribbean and eastern Pacific, the species would seem to have been well established before any emergence of the isthmus of Panama.

Callianidea typa differs from *C. laevicauda* in lacking any sign of a linea thalassinica, and in having bifurcating pleopodal accessory respiratory filaments that divide up to three times. These features were not thought sufficient to justify separation into two genera, even though these two taxa formed a sister group to the *Crosniera-Mictaxius-Thomassinia* group of genera (see Fig. 25).

Crosniera, new genus

Type species.—By present designation, *Callianassa minima* Rathbun, 1901.

Gender.—Feminine.

Diagnosis.—Carapace with subvertical setal row anterolaterally; linea thalassinica not reaching posterior margin of carapace; rostrum narrowly triangular in dorsal view, just overreaching eyestalks. Abdomen somewhat dorsoventrally compressed. Abdominal somite 1 lacking forwardly-directed lobes; somites 1–5 each with single setal row; somite 6 with 3 setal rows. Mandibular incisor toothed. Maxilliped 1, endopod of 2 articles. Maxilliped 2, exopod well developed. Maxilliped 3, pediform but articles showing some broadening; exopod moderately well developed; dentate ischial crest present. Pereopods lacking setal rows. Pereopod 1, chelipeds subsimilar. Pereopod 3, propodus broadened. Pleopodal rami relatively narrow, about 3–4 times longer than greatest width; rami lacking accessory respiratory filaments. Pleopod 2 in male with appendix interna articulating on appendix masculina. Lateral uropodal ramus not bilobed.

Remarks.—De Saint Laurent (1979) diagnosed the genus *Thomassinia* as having the exopod of maxilliped 3 vestigial or absent, and lacking a dentate ischial crest; in *Crosniera minima* the exopod is moderately well developed, as is the dentate crest. The rostrum in *C. minima* is well developed

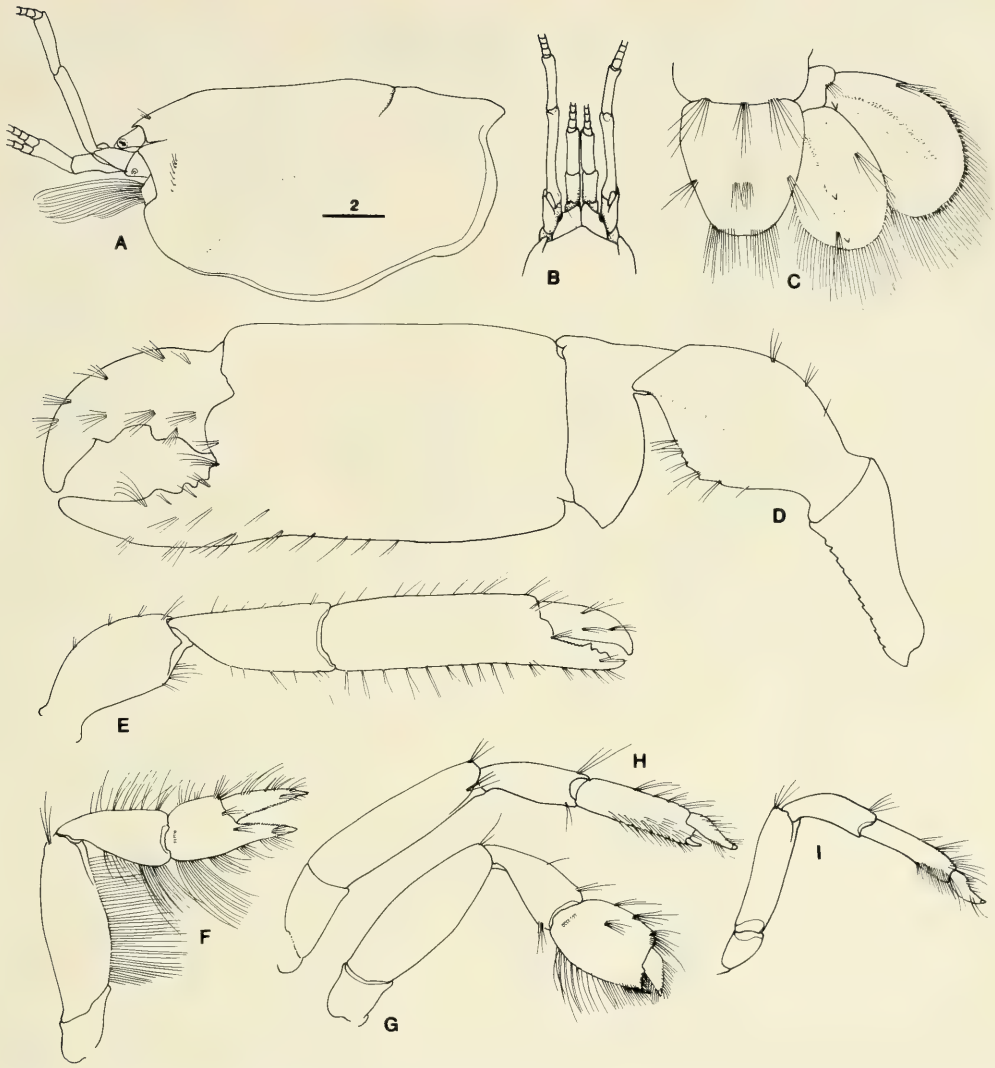


Fig. 3. *Callianidea laevicauda*: A, Carapace in lateral view, scale in mm; B, Anterior carapace, eyes, and bases of antennules and antennae; C, Telson and right uropod; D, Pereopod 1, larger cheliped; E, Pereopod 1, smaller cheliped; F, Pereopod 2; G, Pereopod 3; H, Pereopod 4; I, Pereopod 5.

compared to that of *T. gebioides,* where it is practically lacking. The pereopodal epipods are bifid in *T. gebioides* (G. Poore, 1990, in litt.), but not in *C. minima.* (The upper ramus of these bifid epipods is probably the remnant of a podobranch.) Pleopod 1 of the male is said to be absent in *Thomassinia.* Of seven males of *C. minima* examined, only one possessed first pleopods. Whether this is an aberration, or a function of maturity, is unknown, and can only be resolved with considerably more male material.

Etymology.—The genus is named for Alain Crosnier, ORSTOM scientist at the Muséum National d'Histoire Naturelle, Paris, renowned carcinologist and valued colleague.

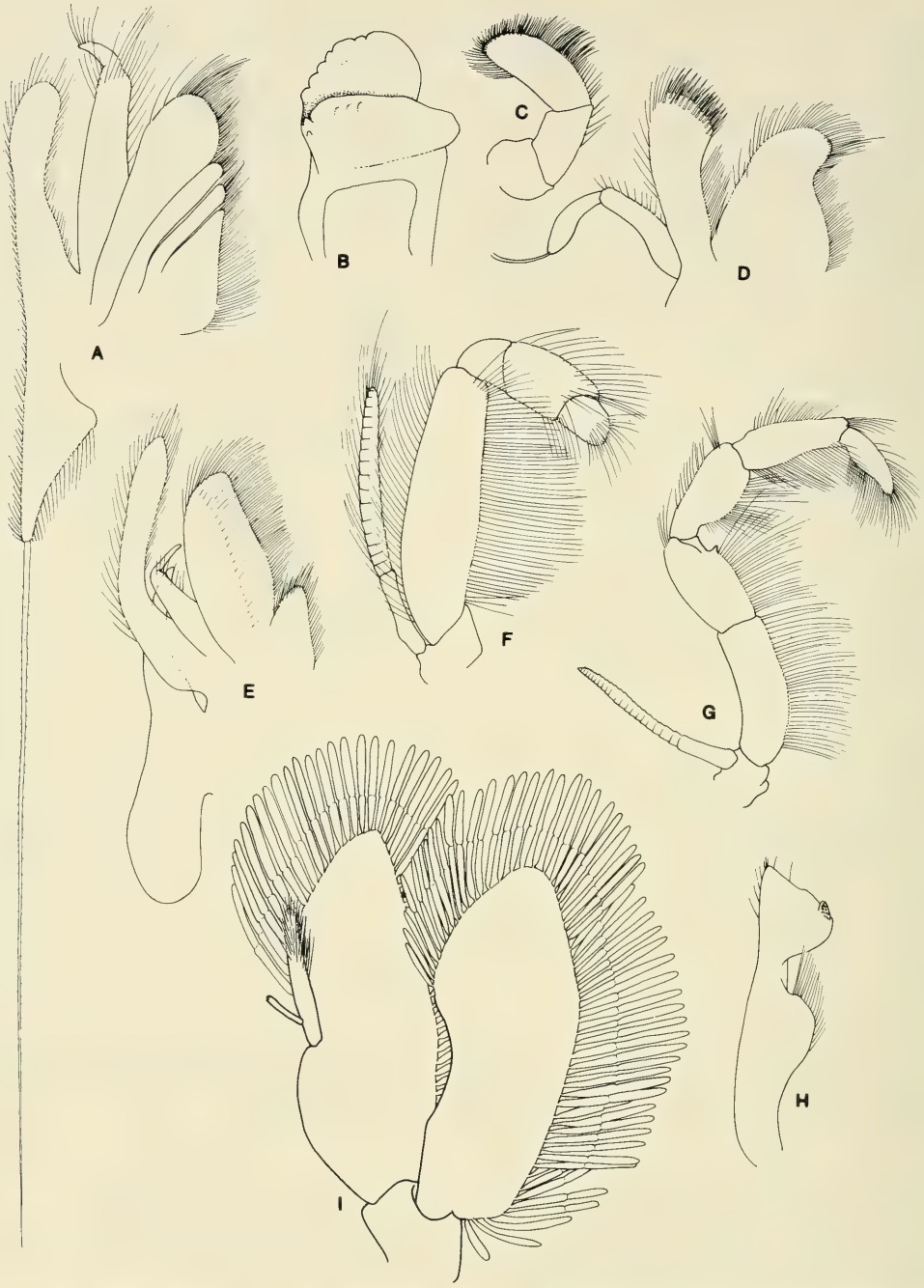


Fig. 4. *Callianidea laevicauda*: A, Maxilla 2; B, Mandible; C, Mandibular palp; D, Maxilla 1; E, Maxilliped 1; F, Maxilliped 2; G, Maxilliped 3; H, Pleopod 1, male; I, Pleopod 2, male.

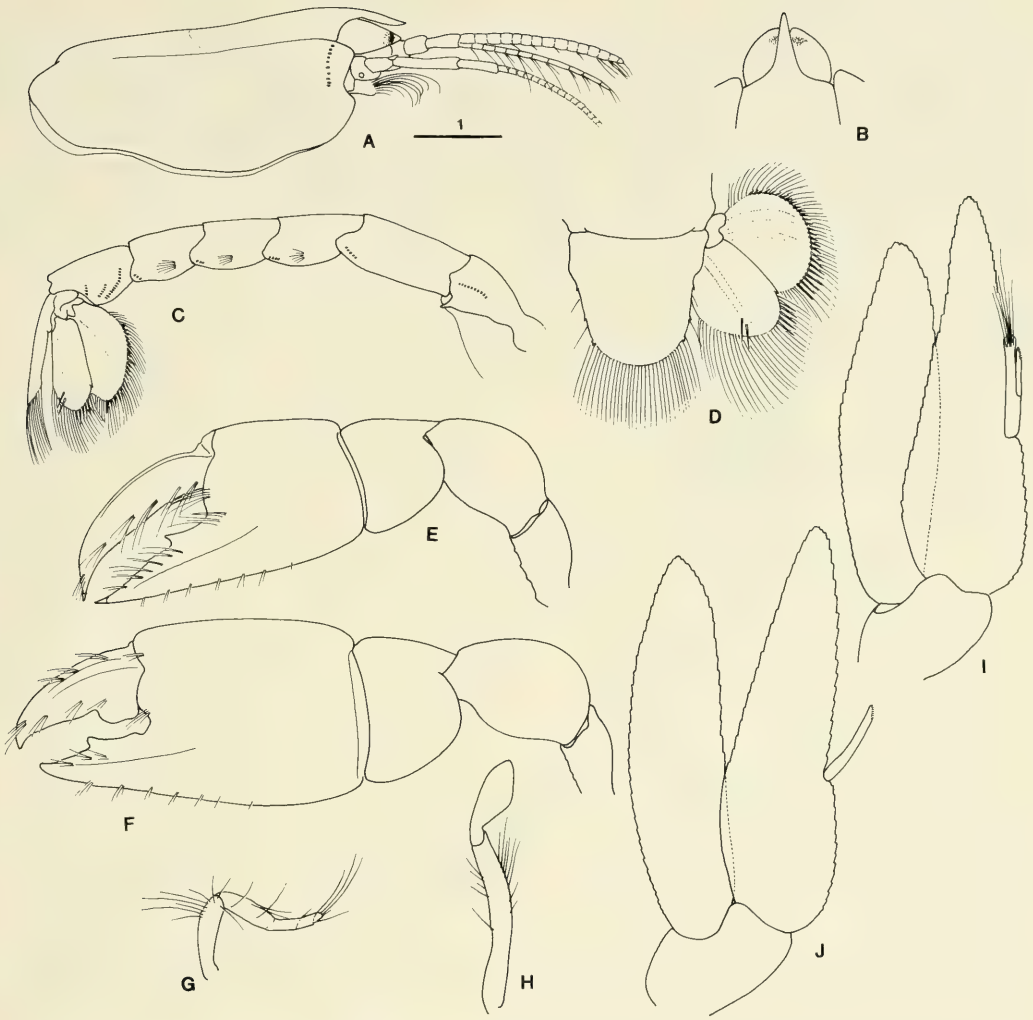


Fig. 5. *Crosniera minima*: A, Carapace in lateral view, scale in mm; B, Rostrum and eyes in dorsal view; C, Abdomen in lateral view; D, Telson and right uropod; E, Pereopod 1, smaller cheliped; F, Pereopod 1, larger cheliped; G, Pleopod 1, female; H, Pleopod 1, male; I, Pleopod 2, male; J, Pleopod 3.

Crosniera minima (Rathbun, 1901)
Figs. 5, 6, Table 1B

Callianassa minima Rathbun, 1901:92, fig. 16.—Schmitt, 1935:5.—de Saint Laurent, 1979:1396.—Manning, 1987:397.

Material examined.—Syntypes, USNM 23779, ♂ cl 2.5 mm, ♀ cl 2.5 mm, *Fish Hawk* sta 6066, Mayaguez Harbor, Puerto Rico, 295–315 m.—USNM 24668, ♀ cl 2.5 mm, *Fish Hawk* sta 6062, Mayaguez Harbor, Puerto Rico, 45-55 m.—USNM 243547, IEC (Interstate Electronic Corp.) sta A7-3, ♀ cl 3.8 mm, Puerto Rico, 18°29′10.8″N, 66°09′6.6″W, 31 m, 11 Jun 1980.—USNM 243533, IEC sta A20-1, ♂ cl 3.1 mm, ♀ cl 3.0 mm, Puerto Rico, 18°30′42″N, 66°08′47.4″W, 295 m, 11 Jun 1980.—USNM 243534, IEC sta SJA-2, ♂ cl 3.9 mm, Puerto Rico, 18°30′42″N, 66°09′19.8″W, 274 m, 10 Jun 1980.—USNM 243543, IEC sta 731 SJ-010-008, ♂ cl 3.0 mm, Puerto Rico, 18°30′42.0″N, 66°11′36.0″W, 282 m, 10 Jun 1980.—USNM 243542, IEC sta 732

Fig. 6. *Crosniera minima*: A, Mandible; B, Maxilla 1; C, Maxilla 2; D, Maxilliped 1; E, Maxilliped 2; F, Maxilliped 3; G, Pereopod 3; H, Pereopod 4; I, Pereopod 2.

SJ-003-006, ♂ cl 3.0 mm, off Mobile, Alabama, 30°09′36″N, 88°06′37″W, 12 m, 29 Jun 1980.—USNM 243539, IEC sta 732 SJ-002-002, ♀ cl 3.2 mm, off Mobile, Alabama, 30°09′24.6″N, 88°05′24.0″W, 10 m, 28 Jun 1980.—USNM 243538, IEC sta 732 SJ-008-008, ♂ cl 2.8 mm, 1 juv., off Mobile, Alabama, 30°09′23″N, 88°08′14″W, 13 m, 28 Jun 1980.—USNM 243540, IEC sta MO-722-408-010, 1 juv., off Mobile, Alabama, 30°09′25″N, 88°08′30″W, 16 m, 19 Jan 1980.—USNM 243541, IEC sta 731 SJ-004-003, ♂ cl 3.0 mm, Puerto Rico, 18°30′36″N, 66°09′36″W, 276 m, 10 Jun 1980.—USNM 243535, IEC sta 731 SJ-004-009, ovig. ♀ cl 3.0 mm, Puerto Rico, 18°30′30″N, 66°09′31.8″W, 264 m, 10 Jun 1980.—USNM 243537, IEC sta 731 SJ-001-007, 2+ cl 2.5 mm, 3.2 mm, 1 juv., Puerto Rico, 18°30′42″N, 66°09′10.2″W, 302 m, 11 Jun 1980.—USNM 243536, IEC sta 731 SJ-008-004, 1 juv., Puerto Rico, 18°30′42″N, 66°10′31.2″W, 298 m, 11 Jun 1980.

Description.—Rostrum slender, acute, just reaching beyond eyes, directed anteroventrally, with faint middorsal keel; linea thalassinica reaching posteriorly from postorbital margin for ⅘ of carapace length; vertical row of setal pits in antennal region of anterior carapace; cervical groove barely demarked. Abdominal somites dorsoventrally flattened; in dorsal view, somite 1 narrow, widening posteriorly, posteroventral angle acute, bearing row of setal pits; somites 2–5 of similar width, pleura posteroventrally rounded with few setal pits; somite 2 longest, somite 6 posteriorly narrowed, with 3 separate rows of setal pits. Telson with 3 small lateral teeth, posterior margin broadly convex.

Eyes flattened, dorsally calcified with sharp lateral margin, cornea not defined, but distal dark pigment visible. Antennule with peduncle article 3 reaching distal margin of antennal article 4; flagella subequal in length, dorsolateral flagellum about twice width of ventromesial one. Antennal acicle reduced to tiny scale; peduncle article 4 twice length of article 5. Lateral epistome bearing numerous elongate downcurved setae. Mandible with incisor bearing 6 corneous marginal teeth; molar with mesial tubercle; palp of 3 articles, article 3 longest, with dense distal setae. Rest of mouthparts as figured (Fig. 6). Maxilliped 2, dactylus bearing cluster of distal spines; exopod well developed. Maxilliped 3, ischium with strong dentate crest on mesial surface; posterior margin bearing dense fringe of setae; merus somewhat expanded, with 2 small teeth on posterior margin; dactylus ovate, strongly setose; exopod reaching distal margin of ischium, bearing few distal setae. Pereopod 1, chelipeds not sexually dimorphic; chelipeds dissimilar, one slightly wider and longer than other; larger cheliped, propodus carinate along anterior and posterior margins, strong oblique ridge on lateral and mesial surface of palm running onto fixed finger, latter with single tooth at about midlength of cutting edge; dactylus with strong proximal tubercle on cutting edge. Smaller cheliped, propodus carinate along anterior and posterior margins, strong oblique ridge on lateral and mesial surface of palm running onto fixed finger, latter with single proximal tooth on cutting edge; dactylar cutting edge unarmed. Pereopod 2 chelate, articles flattened and strongly setose; cutting edges of propodal fixed finger and dactylus bearing close-set row of hyaline truncate teeth. Pereopod 3, propodus and dactylus strongly setose, propodus broadly ovate, flattened, with single posterodistal spine. Pereopod 4, propodus flattened but more elongate than in pereopod 3, posterior margin strongly setose and with single posterodistal spine; dactylus strongly setose. Pereopod 5 lost in all specimens. Pleopod 1 in female uniramous, proximal article shorter than flexed indistinctly segmented distal article. Pleopod 1 in male of 2 articles, proximal article slender, elongate, distal article about half length of proximal, slightly expanded. Pleopod 2 in male with appendix masculina situated almost at midlength of

mesial margin of endopod, rod-shaped and bearing numerous distal setae; appendix interna articulating at midlength of appendix masculina, not reaching apex of latter; pleopods 3–5 with appendix interna on endopod. Lateral ramus of uropod subcircular in outline, bearing marginal plumose setae; mesial ramus ovate, not lobed, bearing marginal setae.

Marcusiaxius Rodrigues & Carvalho, 1972

Marcusiaxius Rodrigues & Carvalho, 1972: 357.

Type species.—By monotypy, *Marcusiaxius lemoscastroi* Rodrigues & Carvalho, 1972.

Gender.—Masculine.

Diagnosis.—Rostrum at same level as anterior carapace, bearing dense anterodorsal submarginal pile of setae, middorsally with flattened triangular area. Carapace with subvertical setal row in postorbital/postantennal region, few setal pits just below lateral carina, subvertical lateral row just anterior to cervical groove. Abdominal somite 1 with dorso-horizontal setal row; somite 2 with ventro-horizontal, and subvertical posterior setal row; somites 3–5 each with subvertical setal row; somite 6 with 3 setal rows. Dense patches of setae on somites 3–5.

Eyestalk apically subacute, shorter than rostrum; corneal area small, subapical. Antennal acicle half or less than half length of antennal peduncle article 4. Maxilliped 3, exopod reduced or absent; merus lacking spine on posterior margin. Pereopod 1, chelae symmetrical. Pereopod 2 with short proximal setal row on lateral surface of propodus. Pereopod 3 with 2 subparallel proximal setal rows on lateral surface of propodus. Pereopod 4, propodus with setal row along anterior margin. Pleopod 1 in ♂ uniramous, of 2 articles, distal article plow-shaped. Pleopod 2 in ♂ with appendix masculina considerably longer than appendix interna. Pleopods 2–5, rami broad. Mesial uropodal ramus strongly produced distolaterally; lateral ramus slightly produced distolaterally. Telson wider than long, lacking non-articulating dorsal spines.

Remarks.—While *Marcusiaxius* and *Meticonaxius* share a number of characters, and appear to be closely related, species of the two may be distinguished on a number of features, as summarized in Table 2.

Key to Species of *Marcusiaxius*

1. Exopod of maxilliped 3 present; Exopod of maxilliped 2 well developed ..... *M. colpos*
– Exopod of maxilliped 3 lacking; Exopod of maxilliped 2 reduced .... *M. lemoscastroi*

Marcusiaxius colpos, new species
Figs. 7, 8, Table 1C

Material examined.—Holotype, USNM 243404, ♂ cl 13.8 mm, MAFLA sta 2534 G, Gulf of Mexico, 29°40′N, 86°17′W, coarse sand, 73 m.—Paratype, USNM 243405, ♂ cl 14.5 mm, MAFLA sta 2533 A, Gulf of Mexico, 29°42′59.9″N, 85°15′28.6″W, coarse sand, 67 m.—USNM 243406, ? sex, (anterior carapace only), MAFLA sta 2644 F, Gulf of Mexico, 29°36.2′N, 87°23.5′W, medium sand, 75 m.—USNM 243407, ♂ cl 17.0 mm (abdomen missing), MAFLA sta 2747-08, ♀ (carapace damaged), sta 2747-06, Gulf of Mexico, 27°24.2′N, 84°07.3′W, medium fine sand, 74 m.—USNM 243410, juv. cl 4.5 mm, BLM 1974, crustacea 31/F.—USNM 243411, juv. cl 5.1 mm, MAFLA sta 2533 F, Gulf of Mexico, 29°42′59.9″N, 85°15′28.6″W, coarse sand, 67 m.—USNM 243412, juv. cl 3.2 mm, MAFLA sta 2211-10, Gulf of Mexico, 27°56′29.5″N, 83°52′59.5″W, coarse sand, 43 m.—USNM 243413, 2 juv. cl 5.9 mm, 9.8 mm, MAFLA sta 2427 C, 28°49′59.1″N, 85°37′01.9″W, clayey sandy silt, 175 m.

Diagnosis.—Carapace with vertical setal row anterior of weakly defined cervical groove, less compact row just ventral of lat-

Table 2.—Comparison of *Marcusiaxius* and *Meticonaxius*.

	Marcusiaxius	*Meticonaxius*
Rostrum	With dense anterodorsal pile of setae submarginally	Lacking dense setal pile
	Dorsal flattened triangular region	Middorsal rounded to carinate ridge
Eye	Eyestalk distally pointed	Eyestalk distally rounded or truncate
	Cornea small, discrete	Cornea diffuse
Maxilliped 3	Dentate ischial crest absent	Dentate ischial crest present
Pleuron 2	Anteroventral horizontal, and posterior subvertical setal row present	Posterior subvertical setal row present
Telson	Basal width greater than greatest length	Basal width less than greatest length

eral carina, and short vertical postorbital row; rostrum with submarginal brush of short stiff setae in anterior half; median carina barely demarked, widening posteriorly; lateral carina entire. Abdominal somites having single row of setae-tubercles on pleura 1 and 3–5, 2 rows on pleuron 2, 3 rows on somite 6; dense posteroventral setal patches on 2–5, clumps of dorsolateral setae on 3–5.

Eye with cornea faintly demarked; eyestalk conical. Antennal acicle slightly more than ⅓ length of peduncle article 4. Maxilliped 2 with exopod elongate; maxilliped 3 lacking spine on merus, lacking dentate ischial crest, exopod reaching distally to base of merus. Pereopod 1, merus with small proximal tooth and larger distal tooth on posterior margin; fingers of chela about ¾ length of propodal palm; fixed finger with strong sinuous tooth and few tiny denticles in proximal half of cutting edge; dactylus with proximal emargination in cutting edge. Pereopod 2, merus lacking spines; propodus with short proximal setal row on lateral surface of propodus. Pereopod 3 with 2 subparallel setal rows on lateral surface of propodus. Pereopod 4 with setal row along anterior margin of propodus. Uropod with both rami widening distally, lateral ramus with distolateral corner produced; mesial ramus with distolateral region strongly produced. Telson ⅓ wider than midlength.

Etymology.—The specific epithet is derived from the Greek 'kolpos,' a gulf or bay, and refers to the Gulf of Mexico.

Marcusiaxius lemoscastroi
Rodrigues & Carvalho, 1972
Figs. 9, 10, Table 1D

Marcusiaxius lemoscastroi Rodrigues & Carvalho, 1972:357.—Carvalho & Rodrigues, 1973:553, figs. 1–21.

Meticonaxius lemoscastroi: Coelho, Ramos-Porto, & Koening, 1980:39.—Coelho & Ramos-Porto, 1987:33.—Coelho, 1987:63, 68.

Material examined.—RMNH, ♂ cl 11.0 mm, Mucurici, Fortaleza, Ceara, Brazil, collected by beach seine net, 7 Mar 1968.—USNM 243403, ♂ cl 12.2 mm, *Pillsbury* sta P-758, 11°42.2'N, 69°40.0'W, Gulf of Venezuela, 15-18 m, 27 Jul 68.

Records.—Dredged from the littoral of Amapa, northern Brazil; shallow infralittoral, Gulf of Venezuela.

Diagnosis.—Carapace with rostrum having submarginal band of short stiff setae, median carina narrowly triangular, flattened, widening posteriorly, lateral carina entire. Abdominal pleuron 1 with hooked posteroventral tooth, pleura 2–6 ventrally rounded; pleura 1, 3–5 each with setal row, pleuron 2 with ventral and posterolateral setal row, pleuron 5 with blunt posterolateral lobe; pleuron 6 with 3 setal-rows, pleura 2–5 posteroventrally densely setose.

Antennal acicle slightly more than half length of peduncle article 4. Maxilliped 2 with short exopod; maxilliped 3 lacking exopod, meral spine, and ischial dentate crest. Pereopod 1, merus with strong tooth at mid-

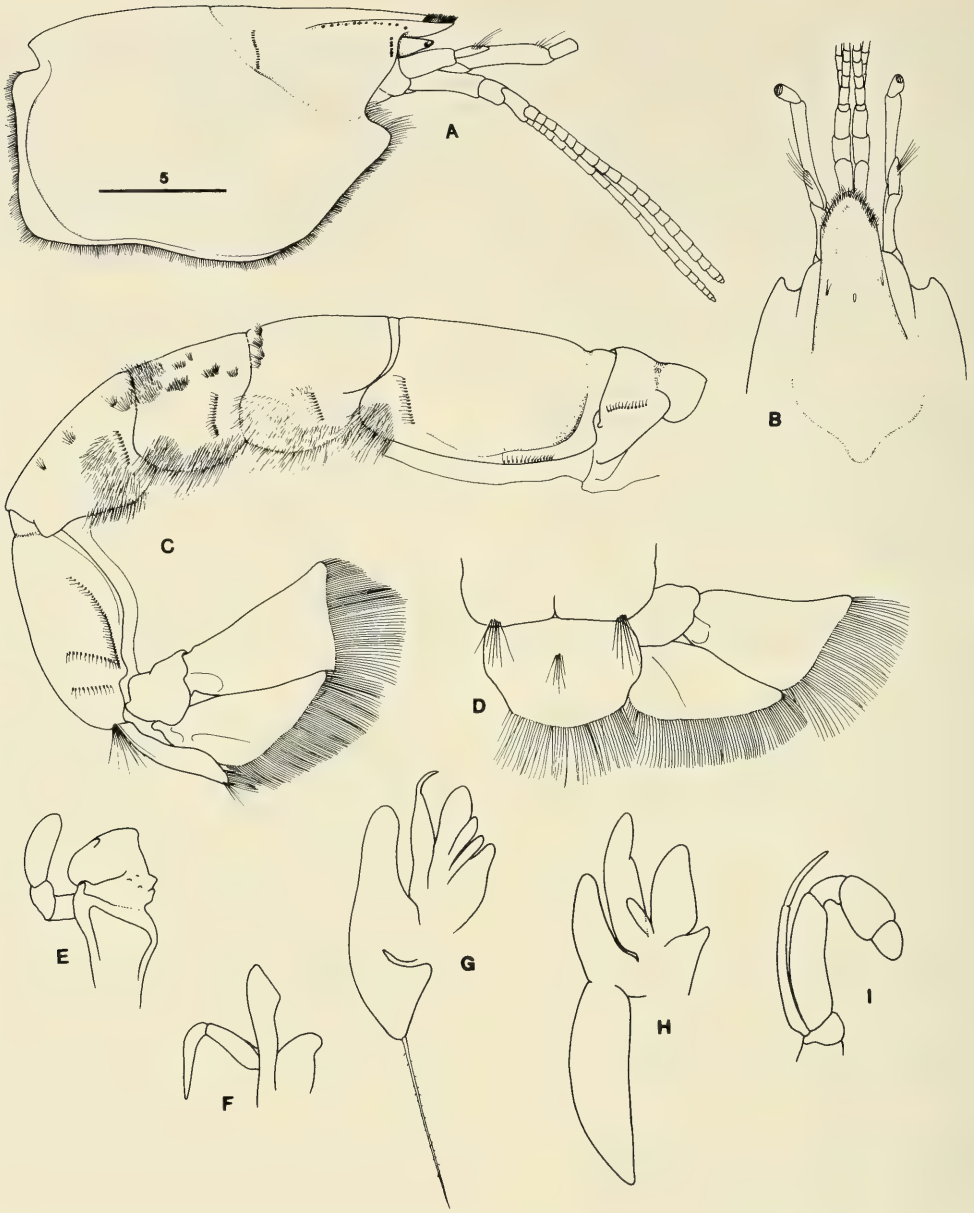


Fig. 7. *Marcusiaxius colpos*: A, Carapace in lateral view, scale in mm; B, Anterior carapace in dorsal view; C, Abdomen in lateral view; D, Telson and right uropod; E, Mandible; F, Maxilla 1; G, Maxilla 2; H, Maxilliped 1; I, Maxilliped 2.

length of posterior margin; fingers slightly shorter than propodal palm, fixed propodal finger with strong triangular tooth in proximal half of cutting edge; cutting edge of dactylus entire. Pereopod 2 lacking meral spines; propodus with short proximal setal row on lateral surface. Pereopod 3, propodus with 2 setal rows on lateral surface. Pereopod 4 with setal row on anterior margin of propodus. Lateral uropodal ramus distolaterally strongly produced; mesial ramus distolaterally produced, considerably wider

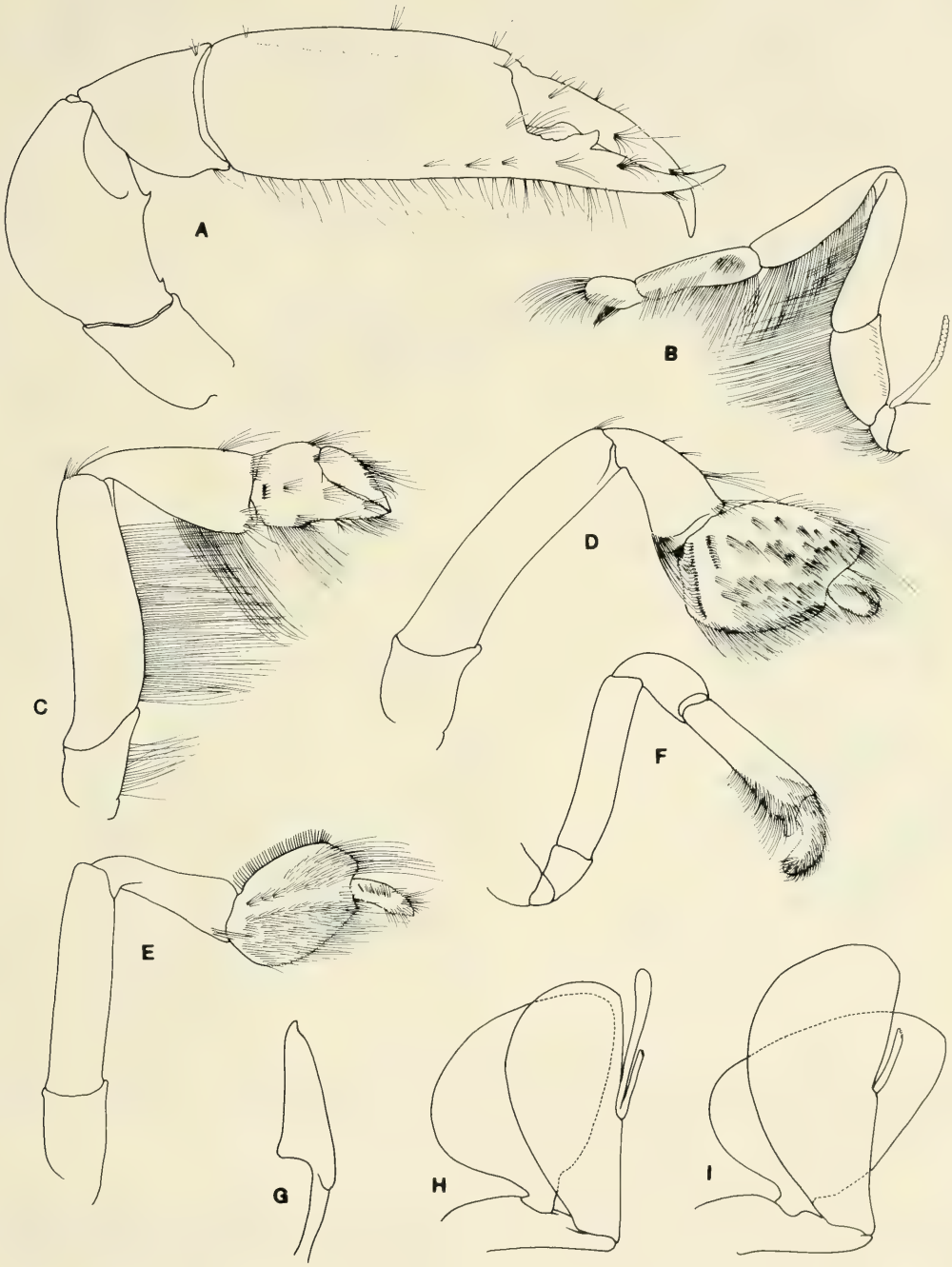


Fig. 8. *Marcusiaxius colpos*: A, Pereopod 1; B, Maxilliped 3; C, Pereopod 2; D, Pereopod 3; E, Pereopod 4; F, Pereopod 5; G, Pleopod 1, male; H, Pleopod 2, male; I, Pleopod 3.

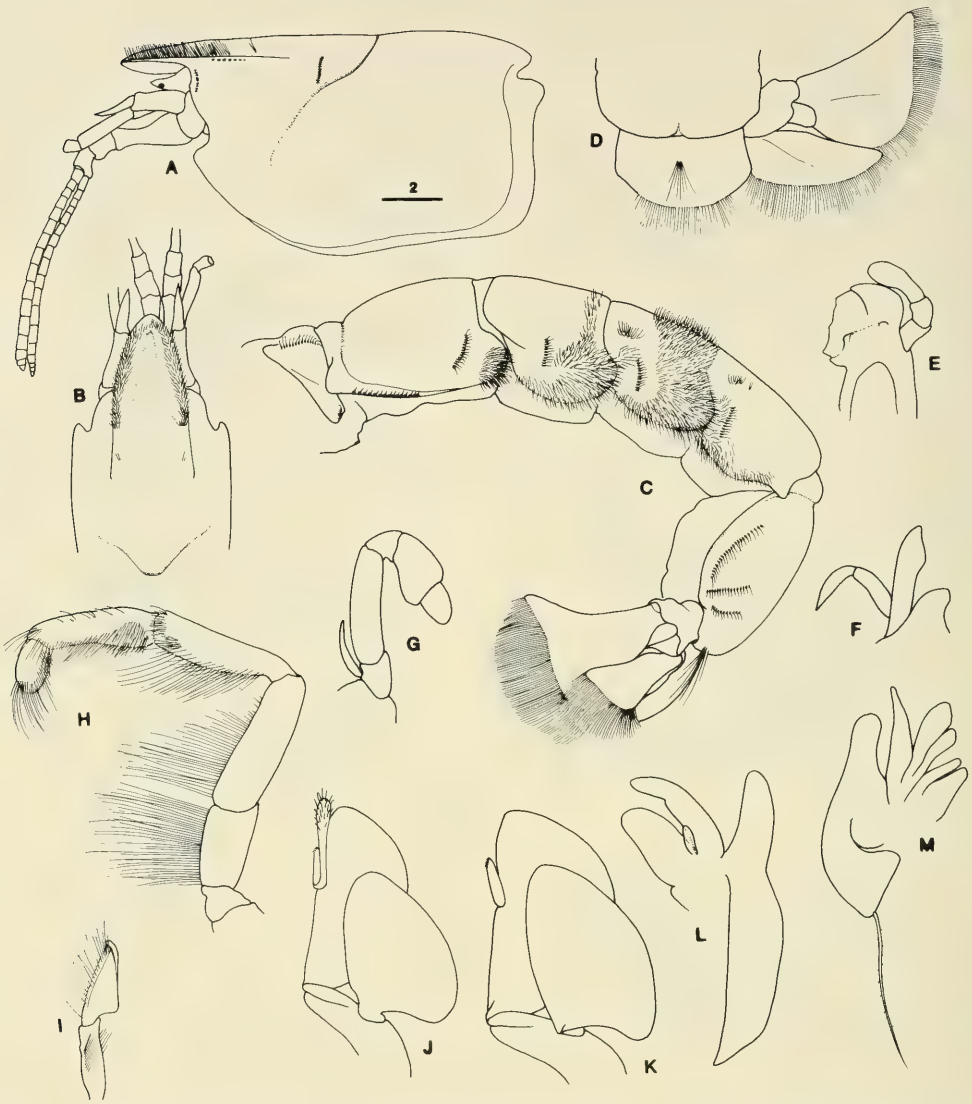


Fig. 9. *Marcusiaxius lemoscastroi*: A, Carapace in lateral view, scale in mm; B, Anterior carapace in dorsal view; C, Abdomen in lateral view; D, Telson and right uropod; E, Mandible; F, Maxilla 1; G, Maxilliped 2; H, Maxilliped 3; I, Pleopod 1, male; J, Pleopod 2, male; K, Pleopod 3; L, Maxilliped 1; M, Maxilla 2.

than long. Telson almost twice wider than long, posterior margin broadly convex.

Meticonaxius De Man, 1905

Meticonaxius De Man, August 1905:592; 1925:5, 53; 1928:18, 21, 30, 53.—Barnard, 1950:499.—Balss, 1957:1579.—Le Loeuff & Intes, 1974:23.—de Saint Laurent, 1973:515, 1979:1397.—Sakai & de Saint Laurent, 1989:9.

Metaxius Bouvier, November 1905:804.—De Man, 1925:8.—Balss, 1957:1582.

Type species.—By monotypy, *Meticonaxius monodon* de Man, 1905:593.

Gender.—Masculine.

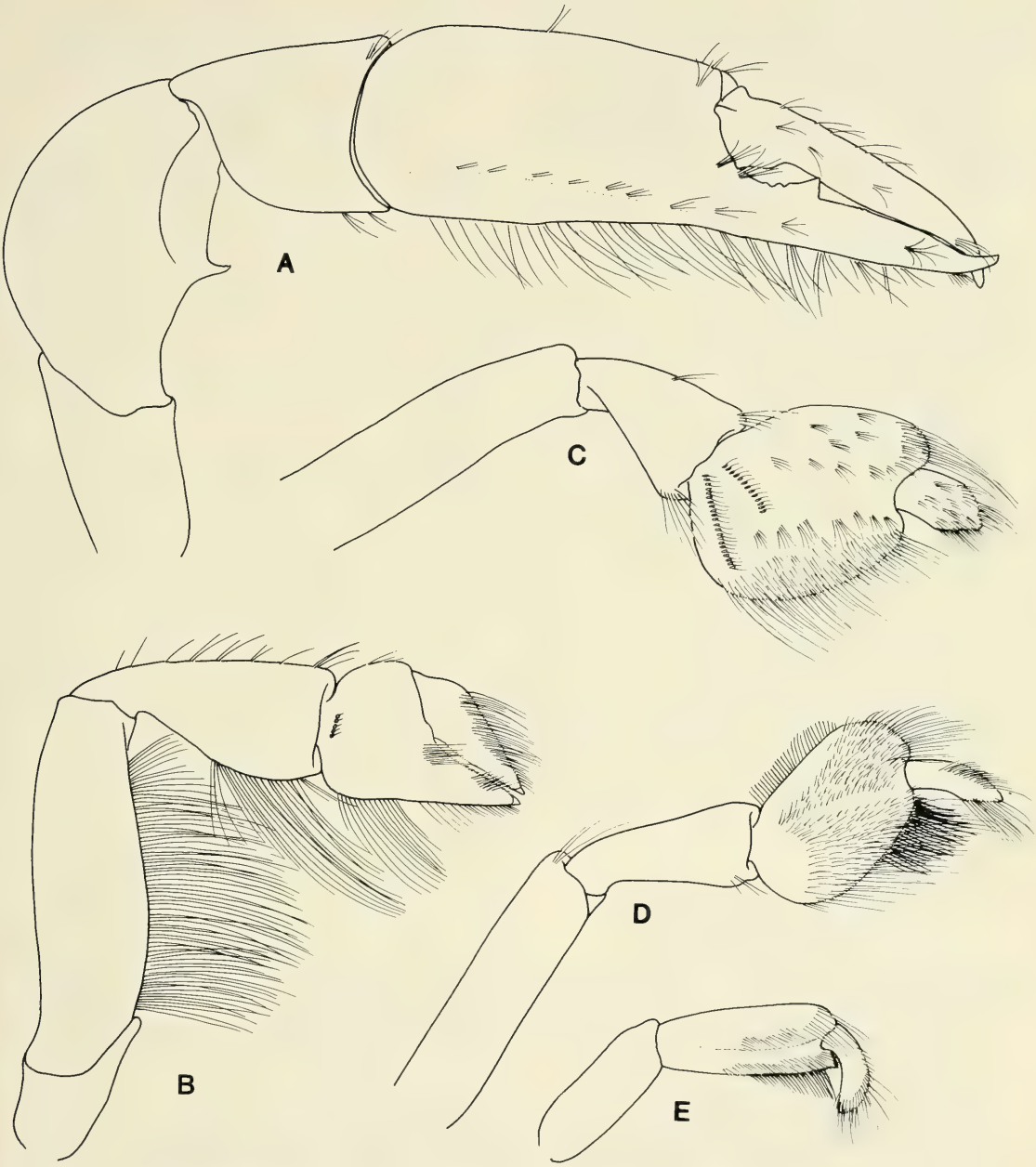


Fig. 10. *Marcusiaxius lemoscastroi*: A, Pereopod 1; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Distal three articles of pereopod 5.

Diagnosis.—Carapace with rostrum at same level as anterior carapace, rostral margins unarmed (single subapical spine on left side in type species may be result of injury). Median carina entire; submedian carina absent; lateral carina entire. Near-vertical setal row on carapace just anterior to cervical groove, less compact setal row immediately ventral to lateral carina; single row of setal pits on abdominal somites 1–5, 3 rows on

somite 6. Abdominal somites 2–4 with posteroventral region of pleura densely setose.

Eye with cornea undifferentiated to poorly differentiated, weakly to moderately well pigmented; eyestalk shorter than rostrum, distally rounded or truncate-flattened. Antennal acicle about half length or less of peduncle article 4. Maxilliped 3 with exopod reduced; meral spine present or absent; dentate ischial crest present. Chelae of pereopod 1 symmetrical. Pereopod 2 chelate, propodus with short proximal setal row. Pereopods 2–4 each with single pleurobranch present (*M. longispina, M. bouvieri,* and *M. monodon*), or pleurobranchs absent (*M. microps*). Propodus of pereopods 3 and 4 expanded, that of pereopod 3 with 1 or 2 setal rows on lateral surface, that of pereopod 4 with single setal row. Pleopodal rami broad; appendix interna on pleopods 2–5. Pleopod 1 in ♂ uniramous, of 2 articles, distal article plow-shaped; pleopod 2 in ♂ with appendix masculina and appendix interna. Lateral uropodal ramus lacking suture, distally broad, occasionally produced distolaterally; mesial ramus distolaterally somewhat produced. Telson longer than wide, lacking non-articulating dorsal spines.

Key to Species of *Meticonaxius* (*M. minutus* excluded due to lack of information)

1. Rostrum apically acute 2
– Rostrum apically rounded 3
2. Merus of pereopod 1 with single spine on posterior margin; Merus of maxilliped 3 with posterodistal spine ..... *M. monodon*
– Merus of pereopod 1 with 2 strong spines on posterior margin; Merus of maxilliped 3 lacking spine ..... *M. bouvieri*
3. Merus of maxilliped 3 with spine . 4
– Merus of maxilliped 3 lacking spine ..... *M. microps*
4. Merus of pereopod 1 with spine on posterior margin ..... *M. capricorni*
– Merus of pereopod 1 lacking spine on posterior margin ... *M. longispina*

Meticonaxius bouvieri, new species
Figs. 11, 12, Table 1E

Material examined.—Holotype, USNM 243408, ♂ cl 16.0 mm.—Paratypes, USNM 243409, 3 ♂ cl 9.8 mm, 10.0 mm, 13.5 mm, 2 ♀ 15.5 mm (abdomen missing), 12.2 mm (abdomen missing), *Pillsbury* sta 1261, off Jamaica, 17°13′N, 77°45′W, 722-768 m. — Paratype, USNM 122453, ♂ cl 5.0 mm, north of Long Island, Bahamas, 23°36′N, 75°25′W, 180–360 m.

Diagnosis.—Carapace smooth; rostrum triangular, midventrally keeled, apically acute/subacute, lateral margins unarmed; median carina reaching posteriorly from rostral apex onto carapace, to about posterior level of lateral carinae. Abdominal pleura ventrally rounded.

Antennal acicle reaching midlength of peduncle article 4. Maxilliped 3, exopod reduced to small lobe; posterior margin of ischium and merus unarmed. Pereopod 1, basis with strong spine on posterior margin; merus with 2 strong spines on posterior margin, anterior margin strongly convex; propodal palm longer than fingers, cutting edge of fixed finger with fine denticulations proximally with slightly larger tubercle, strong acute tooth distal of midlength. Pereopod 2 lacking spination, propodal palm subequal to fingers in length (measured along midline of lateral surface); short proximal setal row on lateral surface of propodus. Pereopod 3 with 2 setal rows on lateral surface of propodus. Pereopod 4 with setal row on anterior margin, plus short proximal row on lateral surface, of propodus. Lateral uropodal ramus distolaterally rounded, not produced; mesial ramus distolaterally slightly produced. Telson slightly longer than greatest width, posterior margin evenly convex.

Etymology.—The species is named for the late Eugène Louis Bouvier, renowned French carcinologist.

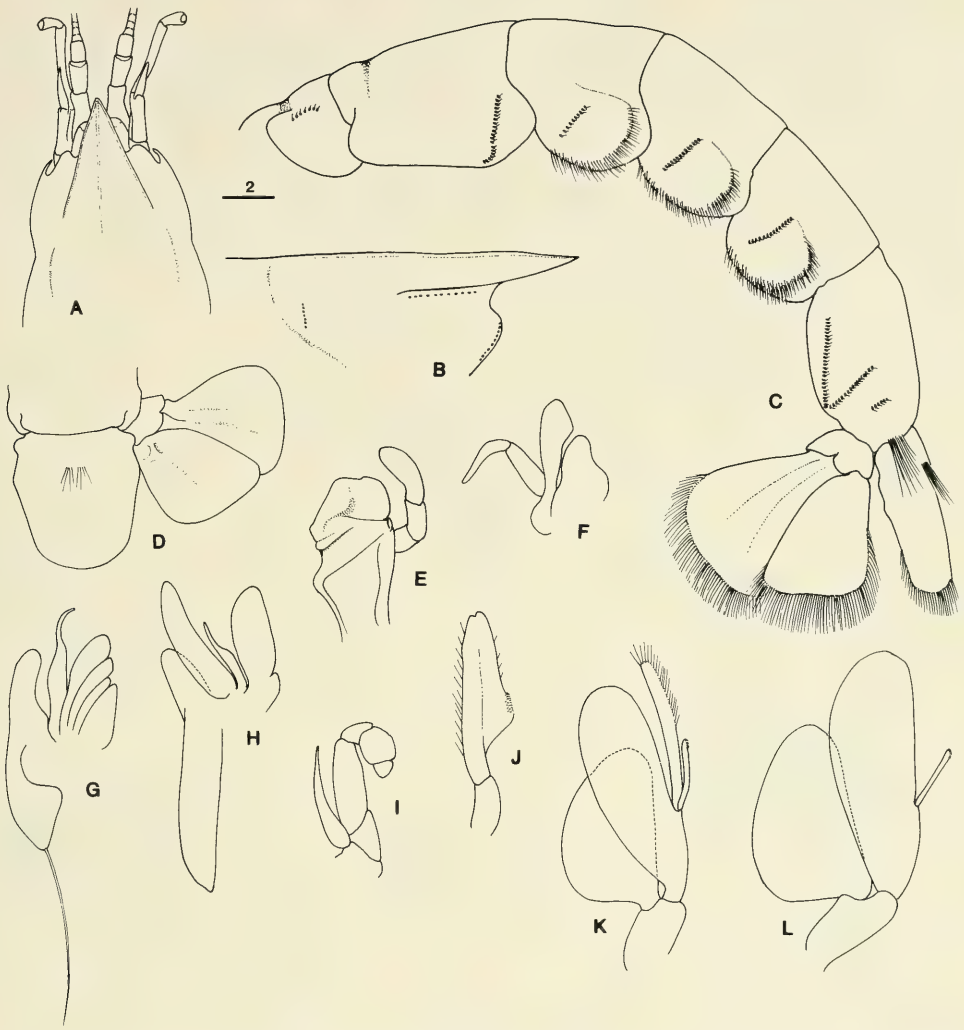


Fig. 11. *Meticonaxius bouvieri*: A, Anterior carapace in dorsal view, scale in mm; B, Anterior carapace in lateral view; C, Abdomen in lateral view; D, Telson and right uropod; E, Mandible; F, Maxilla 1; G, Maxilla 2; H, Maxilliped 1; I, Maxilliped 2; J, Pleopod 1, male; K, Pleopod 2, male; L, Pleopod 3.

Meticonaxius capricorni Coelho, 1987

Meticonaxius capricorni Coelho, 1987:63, 68, figs. 1–3.

Records.—Off Rio de Janeiro and São Paulo states, Brazil, 139–214 m.

Diagnosis.—[Abbreviated; taken from Coelho 1987]: Rostrum subacute, carinate, carina reaching posteriorly onto gastric region of carapace, no raised triangular region. Pleuron of abdominal somite 1 ventrally spinose. Abdominal somites 3–5 having lateral areas of dense setation. Telson basally slightly wider than long, ¾ length of abdominal somite 6.

Maxilliped 3, merus with spine on posterior margin. Pereopod 1, merus with small tooth on posterior margin at about midlength. Pereopod 2, merus lacking spine. Lateral uropodal ramus distally broadened, but not distolaterally produced; mesial ramus distolaterally produced.

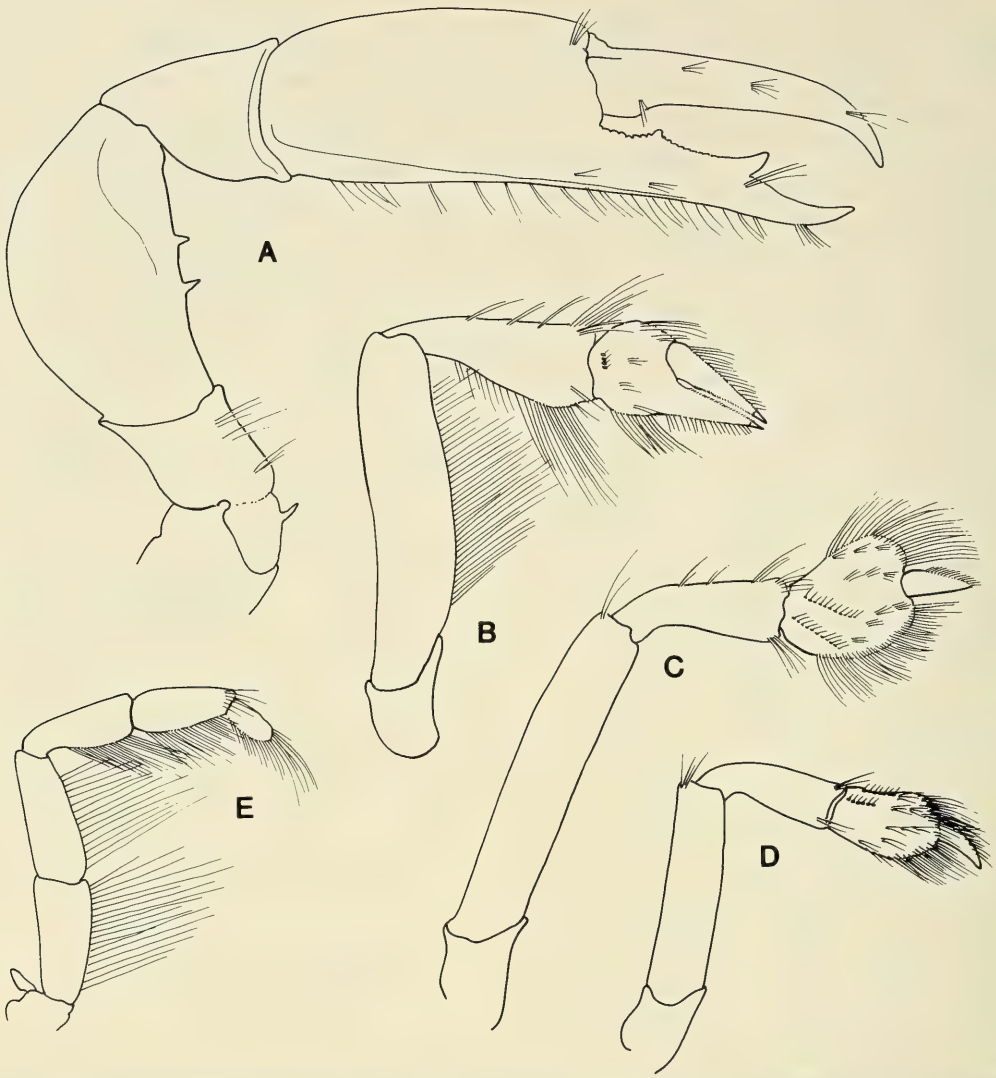


Fig. 12 *Meticonaxius bouvieri*: A, Pereopod 1; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Maxilliped 3.

Meticonaxius longispina
(Stebbing, 1920)
Fig. 13, Table 1F

Axius longispina Stebbing, 1920:265, pls. 106B, 107.
Meticonaxius ?longispina: De Man, 1925:5.
Meticonaxius longispina: Barnard, 1950: 500, fig. 93a–c.—Kensley, 1981:30.—Coelho, 1987:63.

Material examined.—SAM-A2754, juv. ♂ cl 3.8 mm. *Pieter Faure* sta 13039, off East London, South Africa, 91 m.

Records.—Off Cape Morgan (Indian Ocean), South Africa, 95 m.

Diagnosis.—Carapace with rostral apex broadly rounded, margin faintly crenulate; median carina a rounded ridge; lateral carina entire. Abdominal pleuron 1 ventrally acute; pleura 2–6 ventrally broadly convex;

Fig. 13. *Meticonaxius longispina*: A, Carapace in lateral view, scale in mm; B, Rostrum and eyes in dorsal view; C, Abdomen in lateral view; D, Telson and right uropod; E, Maxilla 1; F, Maxilla 2; G, Maxilliped 1; H, Pereopod 1; I, Pereopod 3; J. Pereopod 2; K, Maxilliped 2; L, Maxilliped 3; M, Pereopod 5; N, Pleopod 1, male; O, Pleopod 2, male; P, Pleopod 3.

pleura 1–5 each bearing short row of setose tubercles; pleura 3–5 posteroventrally finely setose; pleuron 6 with longitudinal, and 2 short posterior vertical rows of setose tubercles.

Antennal acicle about ⅓ length of peduncle article 4. Maxilliped 2 with short exopod; maxilliped 3 having merus with single strong non-articulating spine on posterior (mesial) margin; ischial crest having very low teeth; exopod reduced, less than half length of ischium. Pereopod 1, chelae symmetrical; ischium, merus, and carpus unarmed; fingers shorter than propodal palm, fixed finger with single strong triangular tooth slightly beyond midlength of cutting edge; cutting edge of dactylus unarmed. Pereopod 2, merus unarmed; propodal palm somewhat expanded, short proximal setal row on lateral surface. Pereopod 3, propodus with 2 short setal rows on lateral surface. Uropodal rami distally expanded, lateral ramus evenly so, mesial ramus with distolateral part produced more than distomesial; both rami lacking spines. Telson longer than basal width, lacking both articulating and non-articulating spines.

Meticonaxius microps (Bouvier, 1905)
Fig. 14, Table 1G

Metaxius microps Bouvier, 1905:804; 1925: 469, fig. 29.—De Man, 1925:1, 2, 8; 1928: 18, 20, 21, 30.—Balss, 1925:210.—Schmitt, 1935:192, fig. 53.—Balss, 1957: 1582.—Coelho, 1987:63.

Material examined.—Holotype, MCZ, ♂ cl 3.2 mm, *Blake* sta 132, off St. Croix, 210 m.

Diagnosis.—Carapace with rostrum triangular, apically narrowly rounded, with several short marginal setae, margins entire and continuing as entire lateral carina, with broadly rounded median ridge widening posteriorly; subvertical setal row just anterior to cervical groove, plus less compact setal row immediately ventral to lateral carina. Abdominal pleuron 1 with horizontal setal row, ventrally rounded; pleura 2–5 ventrally broadly rounded, each with short vertical row of setose tubercles; pleura 3–5 posteroventrally setose; pleuron 6 with 1 horizontal and 2 vertical rows of setose tubercles.

Eye with cornea faintly demarked, eyestalk conical, shorter than rostrum. Antennal acicle about ⅓ length of peduncle article 4. Maxilliped 2 with reduced exopod; maxilliped 3 lacking exopod. Pereopod 1 (only left cheliped present), merus with small tooth in distal half of posterior margin, fingers shorter than propodal palm, fixed finger with low triangular tooth with midlength of cutting edge; cutting edge of dactylus unarmed. Uropod, both rami distally widened, bearing fringe of plumose setae on distal margins, lacking spines; mesial ramus with distolateral corner produced. Telson lacking spines, longer than basal width, posterior margin convex and bearing fringe of plumose marginal setae.

Meticonaxius minutus Coehlo, 1973

Meticonaxius minutus Coelho, 1973:345; 1987:63, 68.—Coelho & Ramos-Porto, 1987:32.

Records.—Northern Brazil, off Amapá, 89 m; off Cabo Caciporé and Cabo Norte, 89–91 m.

Diagnosis.—[Abbreviated; taken from Coelho 1973:345, and 1987, Table 1]: Rostrum not reaching beyond article 2 of antennal peduncle, with raised triangular region; anterior margin with fringe of setae. Gastric region not carinate. Cornea situated at median part of ocular peduncle. Antennal acicle short. Pleuron of abdominal somite 1 lacking spine. Abdominal somites 3–5 each with lateral area of dense setation. Telson ¾ length of abdominal somite 6.

Meticonaxius monodon De Man, 1905
Fig. 15, Table 1H

Meticonaxius monodon De Man, 1905:593; 1925:5, 54, fig. 10; 1928:20, 21, 30.—Balss, 1925:210.—Coelho, 1987:63.

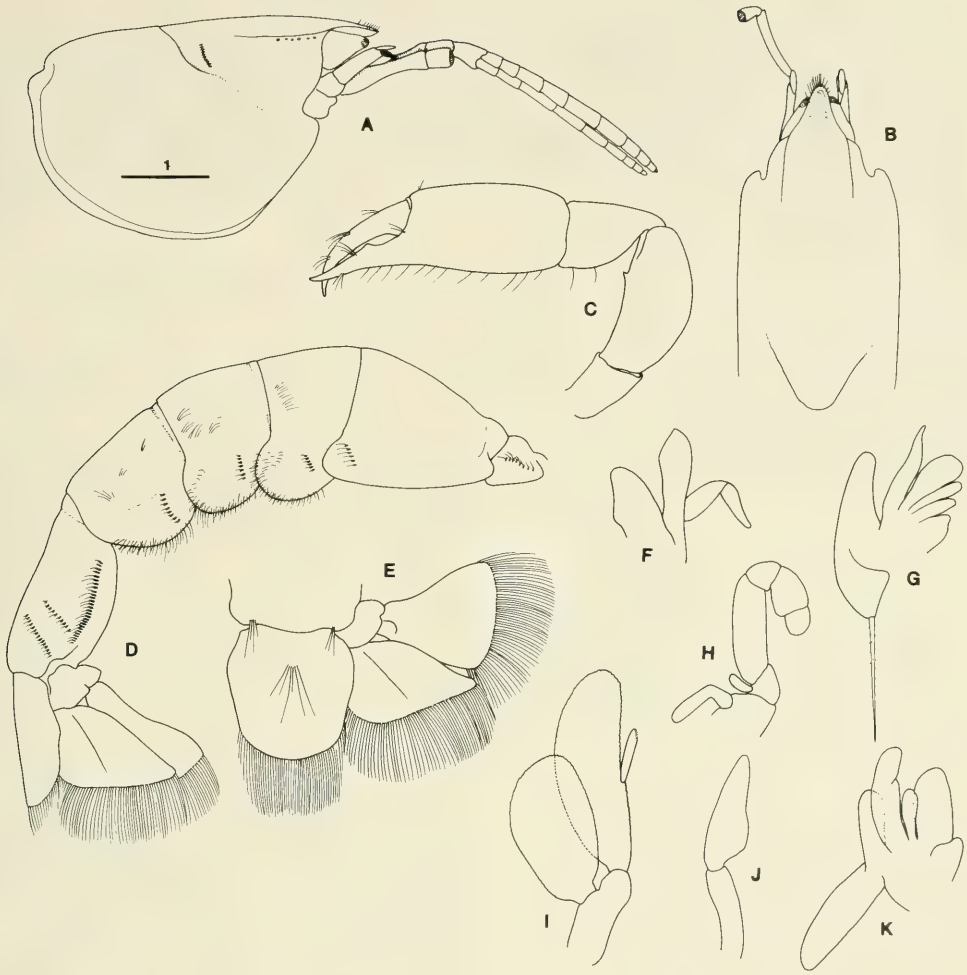


Fig. 14. *Meticonaxius microps,* holotype: A, Carapace in lateral view, scale in mm; B, Anterior carapace in dorsal view; C, Pereopod 1; D, Abdomen in lateral view; E, Telson and right uropod; F, Maxilla 1; G, Maxilla 2; H, Maxilliped 2; I, Pleopod 3; J, Pleopod 1, male; K, Maxilliped 1.

Callianassa (*?Scallasis*) *coeca* Balss, 1925: 212, fig. 16.—De Man, 1928:30.

Material examined.—Holotype, RMNH, ♀ (carapace damaged), north-east of Java, 330 m.

Diagnosis.—Carapace with rostrum apically acute, lacking marginal spines (single subapical spine on left side in holotype perhaps due to injury); median carina entire, rounded ridge; lateral carina entire. Abdominal pleura 1–5 each bearing vertical setal row, pleuron 6 with one longitudinal, and 2 short posterior setal rows; pleuron 1 ventrally narrowly rounded, pleura 2–6 ventrally broadly rounded; pleura 3–5 with posterior part of pleura and dorsolateral part of tergum densely setose.

Antennal acicle reaching slightly beyond midlength of peduncle article 4. Maxilliped 2 with short exopod; maxilliped 3 having very reduced exopod, merus with single distal spine on mesial margin; ischial crest with well defined teeth. Pereopod 1, chelae symmetrical; ischium unarmed; merus with single strong non-articulating spine on posterior margin; carpus and propodal palm smooth, unarmed; fingers shorter than pro-

Fig. 15. *Meticonaxius monodon,* holotype: A, Abdomen in lateral view; B, Anterior carapace in lateral view, scale in mm; C, Anterior carapace in dorsal view; D, Telson and right uropod; E, Maxilla 2; F, Maxilliped 1; G, Maxilliped 3; H, Pereopod 1; I, Pereopod 2; J, Pleopod 2; K, Pereopod 3; L, Pereopod 4; M, Maxilliped 2.

podal palm, fixed finger with strong triangular tooth at midlength of cutting edge, dactylar cutting edge entire. Pereopod 2, merus lacking spines; propodal palm somewhat expanded, with very short setal row proximally on lateral surface. Pereopod 3, propodus somewhat expanded, with single setal row on lateral surface. Pereopod 4,

propodus with single oblique setal row proximally on lateral surface. Uropod with both rami distally expanded and bearing plumose marginal setae, lacking articulating and non-articulating spines. Telson having posterior margin broad, truncate, lacking median, dorsal, and marginal spines.

Michelea, new genus

Type species.—By present designation, *Callianidea vandoverae* Gore, 1987.

Gender.—Feminine.

Diagnosis.—Carapace with 4 setal rows anterior to cervical groove; rostrum short, bluntly triangular; linea thalassinica lacking. Abdominal somites 1–5 each with single setal row; abdominal somite 6 with 2 setal rows. Abdominal somite 1 with lateral anteriorly-directed lobe. Eye distally rounded, cornea poorly defined. Article 1 of antennular peduncle about ½ carapace length. Article 4 of the antennal peduncle about ⅓ carapace length. Antennal scale spiciform, from ½ to ¼ length of peduncle article 4. Lateral epistome with cluster of short setae. Maxilliped 3 pediform, ischium bearing dentate crest; exopod not reduced. Pereopod 1, chelipeds subequal, similar in male and female; merus with anterior margin strongly rounded, posterior margin straight, with fixed tooth at about midlength. Pereopod 2 with proximal setal row on lateral surface of propodus. Pereopod 3 with 2 short proximal setal rows on lateral surface of propodus; latter flattened and somewhat expanded. Pereopod 4 with short proximal setal row on lateral surface of propodus. Respiratory lamellae present on one or both pleopodal rami, lamellae unbranched, of 1 or 2 articles. Uropodal rami lacking suture; lateral ramus not bilobed.

Etymology.—The genus is named for Michèle de Saint Laurent of the Muséum National d'Histoire Naturelle, Paris, renowned carcinologist and respected colleague.

Remarks.—*Callianidea lepta* Sakai, 1987, from Okinawa Island, Japan, differs from *Michelea vandoverae* only in having a much smaller spine on the ischium and merus of pereopod 1, and in lacking any branchial filaments on the pleopodal exopods; it should be included in the genus *Michelea.*

Callianidea leura Poore & Griffin, 1979, from Queensland, Australia, differs from *M. vandoverae* in having simple (not biarticulate) branchial filaments on the pleopods, and in having a reduced exopod on maxilliped 2. It does have article 1 of the antennular peduncle and article 4 of the antennal peduncle elongate and the chelipeds of pereopod 1 subequal, but whether a reduced pleurobranch is present above pereopod 4, is unknown.

Key to Species of *Michelea*

1. Respiratory lamellae present on both rami of pleopods 2–5 2
– Respiratory lamellae present only on endopods of pleopods 2–5 *M. lepta*
2. Respiratory lamellae of pleopods each of single article 3
– Respiratory lamellae of pleopods each of 2 articles ..... *M. vandoverae*
3. Pleopodal exopods bearing few (2–3) respiratory lamellae .. *M. pillsburyi*
– Pleopod exopods bearing many respiratory lamellae along most of margin 4
4. Thoracic gills strikingly reduced; Pleopodal endopods with proximal spiral lamellae-bearing lobe ..... *M. lamellosa*
– Thoracic gills normal, not reduced; Pleopodal endopods lacking basal lobe ..... *M. leura*

Michelea lamellosa, new species
Figs. 16, 17, Table 1I

Material.—Holotype, USNM 243468, ♀ cl 9.6 mm, *Pillsbury* sta P-1215, off Jamaica, 17°36.3′N, 77°02.6′W, 24 m.

Description.—Carapace with cervical groove reaching dorsal midline in posterior

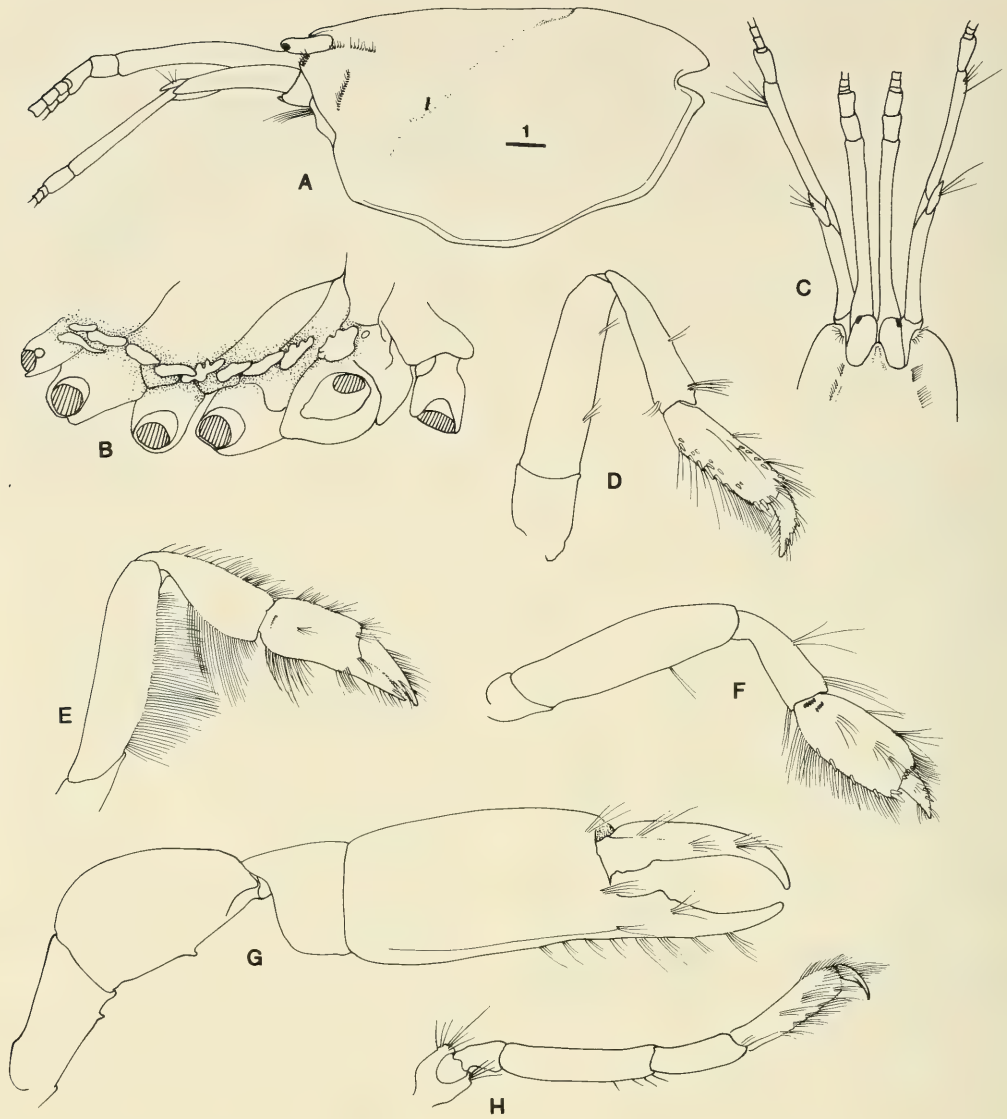


Fig. 16. *Michelea lamellosa,* holotype: A, Carapace in lateral view, scale in mm; B, Left branchial chamber, brachiostegite removed, showing reduced branchiae; C, Anterior carapace, with eyes, and bases of antennules and antennae; D, Pereopod 4; E, Pereopod 2; F, Pereopod 3; G, Pereopod 1; H, Pereopod 5.

half, faintly demarked laterally. Rostrum triangular, with short low middorsal ridge. Row of setal pits on antennal lobe, horizontal row posterior to orbit, subvertical row in postantennal region, shorter vertical row close to lateral cervical groove.

Eyestalk rounded, cornea somewhat demarked, situated distolaterally. Antennular peduncle article 1 elongate-slender, almost reaching midlength of antennal peduncle article 4. Antennal peduncle with acicle short, spiciform, about ¼ length of article 4; article 2 somewhat elongate; article 4 elongate-slender, almost 4 times length of article 5. Lateral epistome with band of short setae reaching anteriorly just beyond antennal ar-

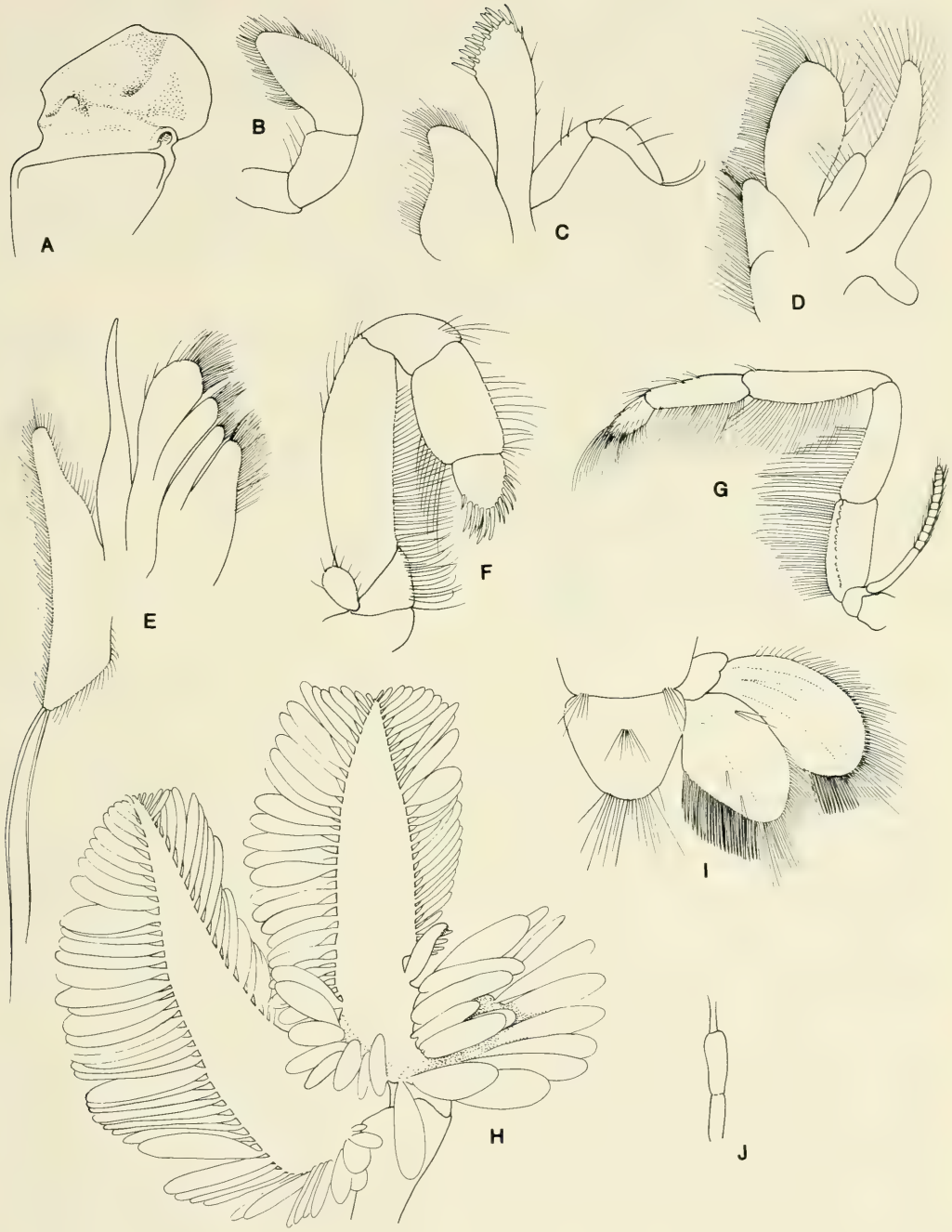


Fig. 17. *Michelea lamellosa,* holotype: A, Mandible; B, Mandibular palp; C, Maxilla 1; D, Maxilliped 1; E, Maxilla 2; F, Maxilliped 2; G, Maxilliped 3; H, Pleopod 2, female; I, Telson and right uropod; J, Pleopod 1, female.

ticle 1. Mandibular incisor with 2 blunt cusps; molar with 2 blunt mesial tubercles; palp of 3 articles, distal article longest, setose. Remainder of mouthparts as figured. Maxilliped 1, endopod of single short article. Maxilliped 2, exopod reduced to short subcircular lobe bearing few setae. Maxilliped 3, posterior margin of merus unarmed. Pereopod 1, chelipeds subequal, ischium with small distal tubercle on posterior margin; merus with small tubercle at about midlength of posterior margin; fingers about ⅔ length of propodal palm, fixed finger with single triangular cusp proximally on cutting edge; dactylus with cutting edge bearing low truncate tubercle proximally, remainder of edge entire. Pereopod 3, propodus flattened, twice longer than wide, with row of 5 spines on posterior margin including posterodistal spine. Pereopod 4, propodus bearing clusters of spines along posterior margin, row of spines along anterior margin. Gills within branchial chamber very reduced, epipods lacking on pereopods.

Pleopod 1 of female uniramous, of 2 articles. Pleopods 2–5 with free appendix interna; bearing densely packed marginal uniarticulate lamellae; endopod proximomesially produced into spiral lobe also bearing lamellae. Pleuron 1 bearing oblique row of setal pits; pleuron 2 with vertical row of setal pits on posterolateral lobe; pleura 3–6 each with vertical row of setal pits at about midlength. Uropodal outer ramus bearing marginal setae plus row of short corneous spines along distolateral margin; both rami bearing dense thickened golden setae-spines along mesial margin. Telson basal width greater than middorsal length, posterior margin broadly rounded, setose.

Etymology.—The specific epithet refers to the lamellate nature of the pleopodal respiratory filaments.

Michelea pillsburyi, new species
Figs. 18, 19, Table 1J

Material.—Holotype, USNM 243469, ♀ cl 3.6 mm, Caribbean off Panama, *Pillsbury* sta P-416, 9°22.6′N, 78°08.4′W, 59 m, 19 Jul 1966.—Paratype, USNM 243470, ♀ cl 4.4 mm, off Atlantic Panama, *Pillsbury* sta P-420, 9°30.5′N, 78°26.0′W, 28 m, 19 Jul 1966.

Description.—Carapace with cervical groove weak, not reaching dorsal midline; rostrum short, triangular. Row of setal pits on antennal lobe, longitudinal row posterior to orbit, few subvertical pits in post-antennal region.

Eyestalk rounded, cornea not demarked. Antennular peduncle article 1 elongate-slender, reaching distally to proximal third of antennal article 4. Antennal peduncle with acicle spiciform, about ¼ length of peduncle article 4; latter elongate-slender, almost 4 times length of article 5. Lateral epistome lacking setae. Mandibular incisor with 2 blunt cusps; molar with 3 mesial rounded tubercles; palp of 3 articles, distal article longest, setose. Remainder of mouthparts as figured. Maxilliped 1, endopod of single short article. Maxilliped 2, exopod reduced to short lobe bearing few setae. Maxilliped 3, merus with strong distal spine on posterior margin. Pereopod 1, chelipeds subsimilar, equal in length, chela of one slightly wider than other; ischium with strong spine in distal half of posterior margin; merus with strong spine at about midlength of posterior margin; fingers about ⅚ length of propodal palm, cutting edge of fixed finger with 3 low evenly-spaced teeth; cutting edge of dactylus entire. Pereopod 3, propodus about 3 times longer than wide, flattened. Pereopod 4, propodus with 3 spines on posterior margin, including distalmost spine. Pereopod 5, propodus with strong posterodistal spine. Pleopod 1 of female uniramous, with faint constriction indicating 2 fused articles. Pleopods 2–5 with free appendix interna, endopod bearing uniarticulate lamellae along lateral margin, exopod bearing 2–3 distal lamellae on lateral margin, remainder of margin setose. Uropodal lateral ramus with small spine on lateral margin, latter setose and bearing row of short corneous

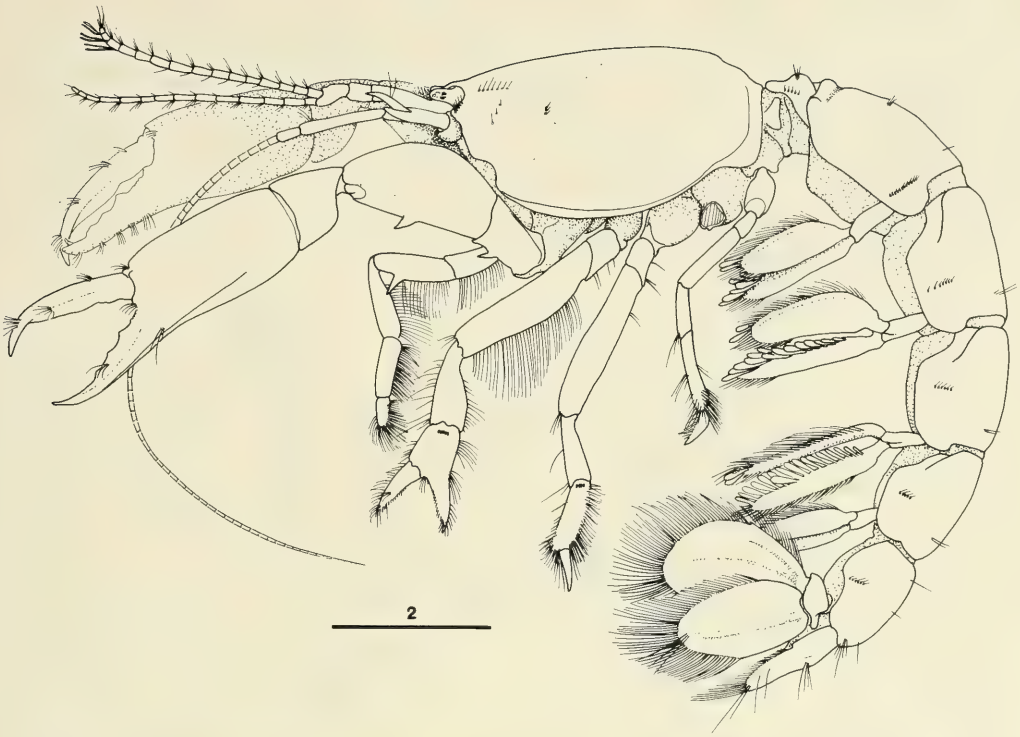


Fig. 18. *Michelea pillsburyi,* holotype, lateral view, scale in mm.

spines; inner ramus bearing numerous marginal setae. Telson length equal to greatest width, posterior margin broadly rounded, setose.

Etymology.—The specific epithet refers to the Research Vessel *Pillsbury,* from which this, and much other valuable crustacean material was collected.

Michelea vandoverae (Gore, 1987)
Figs. 20, 21, Table 1K

Callianidea vandoverae Gore, 1987:186, figs. 1–4.

Material.—USNM 211492, Gulf of Mexico MAFLA sta 2211, 27°56′29.5″N, 83°52′59.5″W, 43 m, coarse sand: sample 2211 A23, ♀ cl 5.7 mm, ♂ cl 4.1 mm; sample 2211 C, juv. cl 2.8 mm; sample 2211 E, ♀ cl 6.2 mm; sample 2211 F22, ♂ cl 6.0 mm; sample 2211 31H, ♂ cl 9.0 mm; sample 2211-07, ♀ cl 10.0 mm.—USNM 211493, Gulf of Mexico, MAFLA sta 2528, 29°54′58.6″N, 86°04′58.5″W, 37 m, coarse sand: sample 2528H, ♂ cl 5.5 mm.

Description.—Cervical groove at about midlength of carapace, reaching dorsal midline. Rostrum moderately well developed, broadly triangular, with 2 low teeth on lateral margin. Irregular row of setal pits in position of lateral carina, short row on antennal lobe, subvertical row in postantennal region, short vertical row just anterior of cervical groove.

Eyestalk rounded, cornea not defined. Antennular peduncle article 1 elongate-slender, reaching distally to about midlength of antennal article 4. Antennal acicle spiciform, almost half length of elongate article 4. Lateral epistome bearing cluster of short setae, not reaching anteriorly beyond level of basal antennal article. Mandibular incisor having 2 blunt cusps; molar with 3–4 rounded tubercles mesially; palp of 3 ar-

Fig. 19. *Michelea pillsburyi,* paratype: A, Anterior carapace, with eyes, and bases of antennules and antennae; B, Carapace in lateral view, scale in mm; C, Telson and left uropod; D, Mandible; E, Mandibular palp; F, Maxilla 1; G, Maxilla 2; H, Maxilliped 1; I, Maxilliped 3; J, Maxilliped 2; K, Pleopod 1, female; L, Pleopod 2, female.

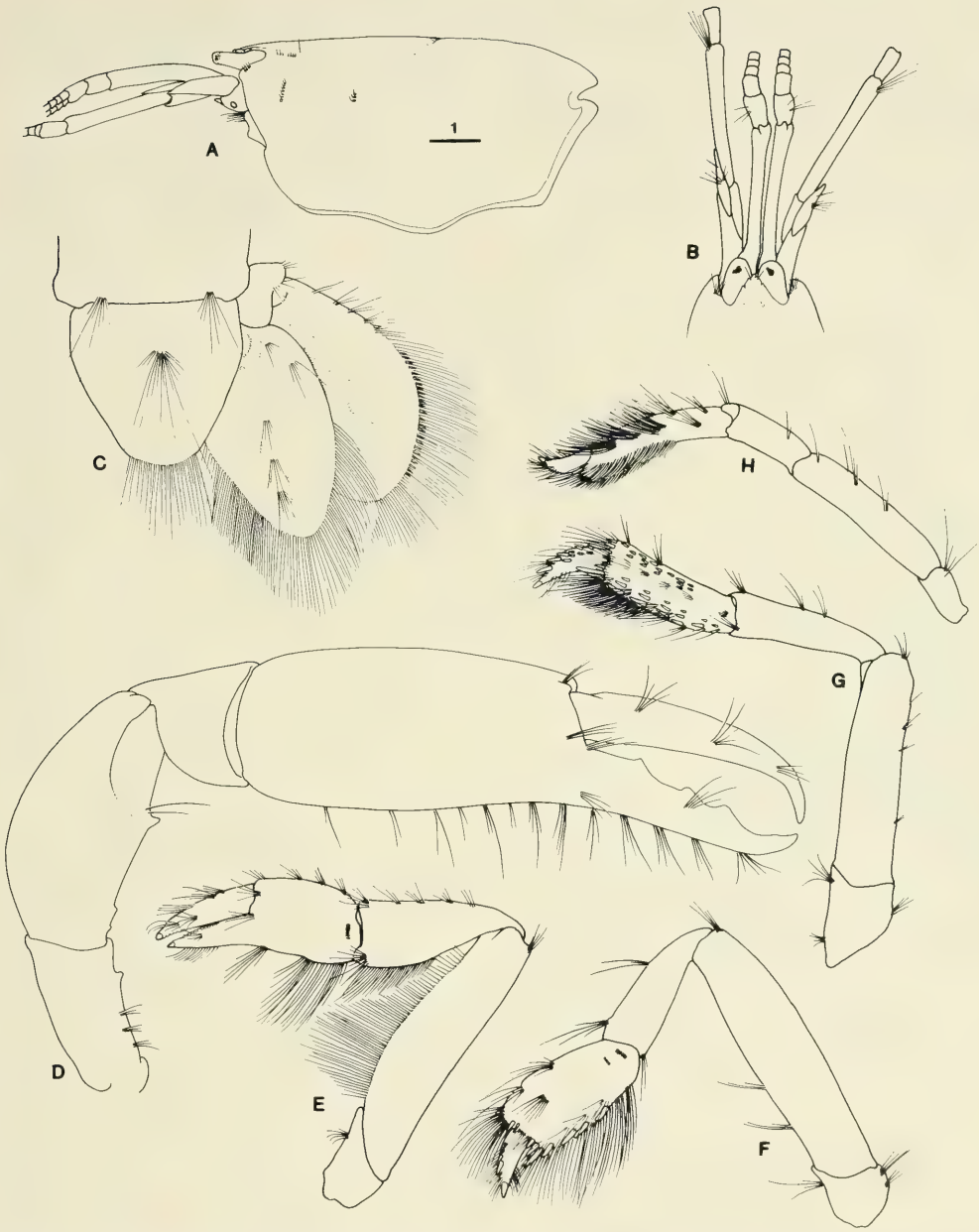


Fig. 20. *Michelea vandoverae*: A, Carapace in lateral view, scale in mm; B, Anterior carapace, eyes, and bases of antennules and antennae; C, Telson and right uropod; D, Pereopod 1; E, Pereopod 2; F, Pereopod 3; G, Pereopod 4; H, Pereopod 5.

ticles, distal article longest, setose. Remainder of mouthparts as figured. Maxilliped 1, endopod with tiny distal article. Maxilliped 2, exopod well developed, with distal segmented flagellum. Maxilliped 3, merus with strong distal spine on posterior margin. Pereopod 1, chelipeds subsimilar, of equal length, propodus slightly broader in one; is-

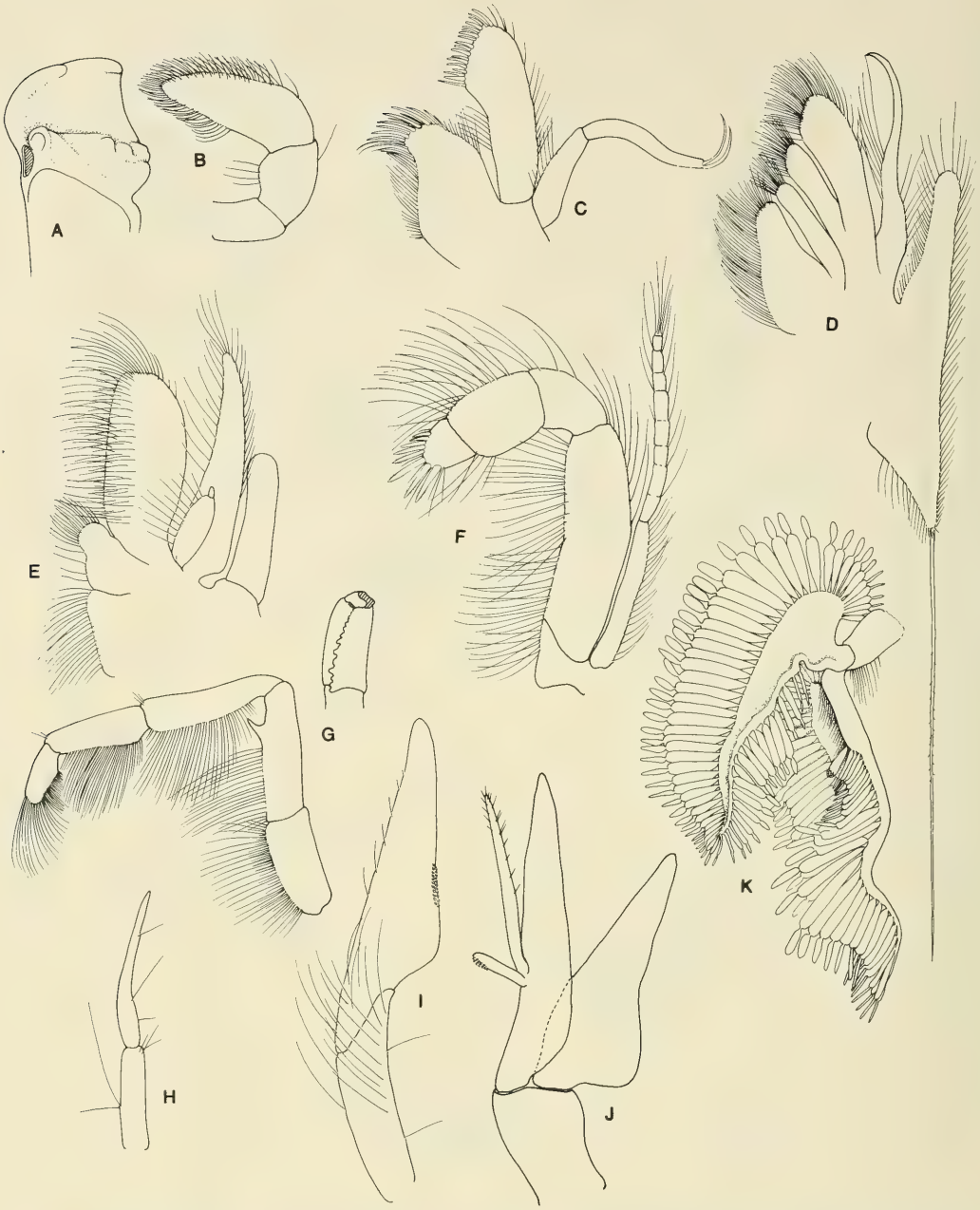


Fig. 21. *Michelea vandoverae*: A, Mandible; B, Mandibular palp; C, Maxilla 1; D, Maxilla 2; E, Maxilliped 1; F, Maxilliped 2; G, Maxilliped 3 with mesial view of ischium; H, Pleopod 1, female; I, Pleopod 1, male; J, Pleopod 2, male; K, Pleopod 3.

chium with 2–3 distal blunt tubercles on posterior margin; merus with single moderately strong blunt spine on posterior margin; propodal palm about one-third longer than fingers, cutting edge of fixed finger with 3 evenly-spaced low triangular teeth; dactylus entire or with low proximal tubercle. Pereopod 3, propodus moderately broad,

flattened, greatest width about 4/7 length, with several spines along posterior and distal margins but not subchelate. Pereopod 4, lateral surface of propodus and dactylus spinose.

Pleopod 1 of female uniramous, of 2 articles, distal article about 1.5 times length of proximal, slender and tapering. Pleopod 1 of male with cluster of tiny hooks on mesial margin of triangular distal article. Pleopod 2 of male with appendix interna and appendix masculina situated at about proximal third of endopod; slender tapering appendix masculina with lateral and distal setae, about 3 times longer than appendix interna. Pleopods 2–5, both rami bearing marginal biarticulate flattened lamellae. Outer uropodal ramus with small non-corneous spine on outer margin just short of midlength, row of tiny corneous marginal spines on outer margin from about midlength to just short of apex; both rami with marginal setae becoming denser and thickened proximomesially. Telson length equal to greatest width, broadly rounded posterior margin setose.

Mictaxius, new genus

Type species.—By present designation, *Mictaxius thalassicola,* new species.

Gender.—Masculine.

Diagnosis.—Carapace lacking carinae; cervical groove barely distinguishable; with linea thalassinica reaching from anterior margin in region of eye to posterior margin; row of setal pits present in anterolateral region; rostrum barely demarked, a low convexity at base of eyestalks. Abdominal somite 1 lacking anteriorly-directed lobes; somites 1–6 each with short setal row.

Eyestalk distally pointed, cornea poorly defined, situated subapically, moderately pigmented. Antennal acicle reduced to small immobile scale. Mandibular incisor toothed. Maxillipeds 1 and 2 with well developed exopod. Maxilliped 1 endopod of 2 articles. Maxilliped 3 exopod vestigial, dentate ischial crest on mesial surface moderately well developed. Pereopod 1, chelipeds asymmetrical, not sexually dimorphic. Pereopods 2–4 each with very short setal row. Propodus of pereopod 3 expanded, subcircular. Pereopods 3–5, dactyli simple. Pleopodal rami somewhat expanded, 2–3 times longer than greatest width; appendix interna present on pleopods 2–5. Pleopod 1 in male absent. Pleopod 1 in female uniramous, of 2 articles. Pleopod 2 in male, appendix masculina and appendix interna fused, resultant lobe-like structure bearing both hooks and elongate setae distally. Telson broader than long, semicircular in outline, lacking spines. Lateral uropodal ramus bilobed, lacking transverse suture.

Etymology.—The generic name is a combination of the Greek 'miktos,' a mixture, and the frequently-used thalassinidean suffix 'axius,' and refers to the seeming mix of callianassid and callianideid features found in the type and only species of this genus.

Remarks.—*Mictaxius* shows several features thought to be advanced amongst the callianideids: antennal acicle very reduced; eyestalk flattened; maxilliped 3 exopod vestigial; linea thalassinica running the full length of carapace. The genus belongs to that group of callianideids that lack respiratory filaments on the pleopods, but the complete linea thalassinica, the fused appendix masculina and appendix interna, and the bilobed outer uropodal ramus (which features appear in the Callianassidae) immediately separate it from the rest of this group.

Mictaxius thalassicola, new species
Figs. 22, 23, 24, Table 1L

Material examined.—Holotype, USNM 243544, ♂ cl 3.9 mm, Paratypes, 3 ♂ cl 2.5 mm, 3.4 mm, 3.9 mm, ovig. ♀ cl 2.5 mm, 2 ♀ cl 3.1 mm, 3.9 mm, Panama Survey sta 115-4, Pico Feo, Atlantic Panama, in shallow-water *Thalassia* patch, 8 Nov 1972.—Paratypes, USNM 243545, 3 ♂ cl 3.1 mm, 3.1 mm, 4.0 mm, ovig. ♀ cl 3.1 mm, 2 ♀ cl 3.4 mm, 3.4 mm, Panama Survey sta 136-

2, Isla Mira, San Blas Islands, Atlantic Panama, in shallow-water *Thalassia* patch, 8 Apr 1973.

Description.—Carapace lacking definite rostrum, anterodorsal margin with slight median bulge, eyestalks completely exposed. Linea thalassinica running full length of carapace; antennal angle of carapace rounded; subvertical setal row situated posterior to antennal region of anterior carapace; cervical groove barely demarked. Abdomen somewhat bilaterally compressed; somite 1, pleuron tapering posteroventrally to acute triangular lobe, with setal row anterolaterally; somite 2 longest, pleuron ventrally broadly convex, with short setal row posteroventrally; somites 3–6 subequal in length, 3–5 each with short setal row posteroventrally; somite 6 with 2 setal rows. Telson semicircular in outline, basally broader than middorsal length.

Eyestalk tapering to narrowly rounded mesiodistal apex, poorly-defined cornea moderately pigmented, situated distal to midlength. Antennule with 3 peduncle articles subequal in length; flagella subequal in length, dorsolateral flagellum broader than ventromesial flagellum. Antennal peduncle with article 4 longest; acicle reduced to tiny immobile scale. Epistome bearing lateral cluster of elongate setae, latter downcurved distally. Mouthparts as illustrated. Mandibular incisor having 9 serrate marginal teeth; molar poorly developed; palp of 3 articles, distal article longest. Maxilliped 2 with relatively well developed exopod. Maxilliped 3, 5 distal articles strongly setose; dactylus broadly ovate; exopod reduced to tiny digitiform process. Pereopod 1, chelipeds dissimilar; larger chela with posterior margin of ischium finely serrate; propodal palm about 1.8 times length of fingers; fixed finger with single triangular tooth on cutting edge; oblique ridge running from palm onto fixed finger on both lateral and mesial surface; dactylus with cutting edge faintly irregular to entire. Smaller cheliped, propodal palm slightly shorter than fingers; fixed finger with small tooth in distal half of cutting edge; oblique ridge running from palm to distal fixed finger on both lateral and mesial surface; dactylus with cutting edge entire. Pereopod 2 chelate, cutting edges of propodal finger and dactylus bearing obliquely-set hyaline spines; propodus with very short proximal setal row on lateral surface. Pereopod 3, propodus broadly ovate, posterior margin densely setose and bearing single distal spine, very short proximal setal row on lateral surface; dactylus setose, slightly less than half length of propodus, tapering distally. Pereopod 4, propodus 2.5 times longer than wide, posterior margin strongly setose, with single distal spine, very short proximal setal row on lateral surface; dactylus about ⅖ length of propodus, strongly setose, tapering distally. Pereopod 5, propodus distally strongly setose; dactylus distally rounded, setose. Pleopod 1 in male absent. Pleopod 1 in female of 2 articles, distal article 1.5 times length of proximal. Pleopod 2 in male with fused appendix masculina/appendix interna articulating at about proximal ⅓ of mesial margin of endopod, bearing cluster of about 8 elongate terminal setae and subapical clump of hooks. Uropod with lateral ramus broadly bilobed, outer lobe bearing marginal spines on distal margin, remainder of margin setose; mesial ramus broadly ovate, with setose margin.

Etymology.—The specific epithet, meaning 'living in *Thalassia*' refers to the fact that all the specimens were collected in shallow beds of this seagrass.

Thomassinia de Saint Laurent, 1979

Thomassinia de Saint Laurent, 1979:1396.

Type species.—By original designation, *Thomassinia gebioides* de Saint Laurent, 1979.

Gender.—Feminine.

Diagnosis.—[Abbreviated, taken from de Saint Laurent 1979]: Carapace with subvertical setal row anterolaterally; linea thalassinica not reaching posterior margin of

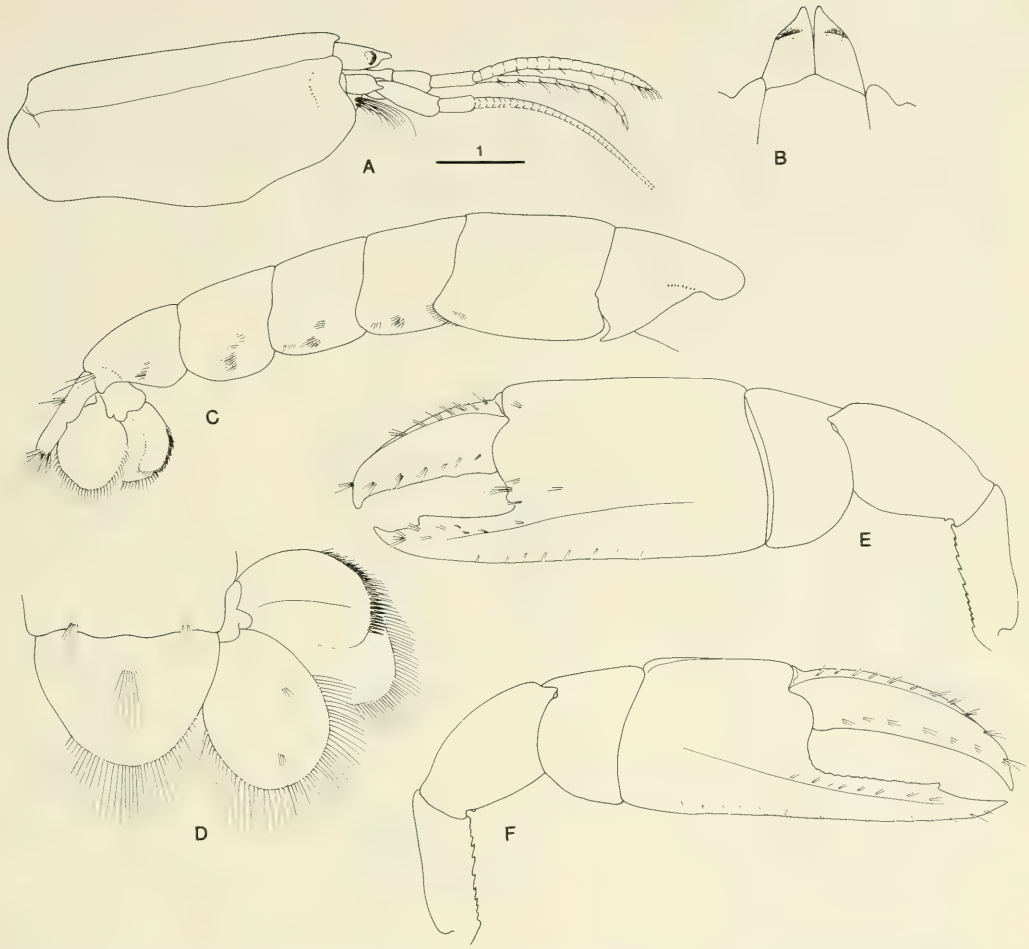


Fig. 22. *Mictaxius thalassicola*: A, Carapace in lateral view, scale in mm; B, Anterior carapace and eyes in dorsal view; C, Abdomen in lateral view; D, Telson and right uropod; E, Pereopod 1, larger cheliped; F, Pereopod 1, smaller cheliped.

carapace; rostrum barely defined, anterodorsal margin of carapace low, triangular. Abdominal somite 1 lacking anteriorly-directed lobes. Antennal acicle vestigial or absent. Mandibular incisor toothed. Maxilliped 2, exopod well developed. Maxilliped 3, articles becoming broadened; exopod vestigial or absent; ischium lacking dentate crest. Pereopod 1, chelipeds subequal. Pereopod 3, propodus broadened. Pleopod 1 in male absent. Pleopods lacking respiratory filaments. Lateral uropodal ramus not bilobed.

Remarks.—*Thomassinia gebioides* de Saint Laurent, 1979, from Madagascar, has not yet been fully described or illustrated, and with no material available, no further morphological information can be provided.

Discussion

In addition to the 17 species either described or mentioned above, the only other species belonging to the family Callianideidae as defined here is *Callianidea planocula* Melin, 1939, from the Bonin Islands, Japan. (*Callianidea elongata* (Guerin-Méneville,

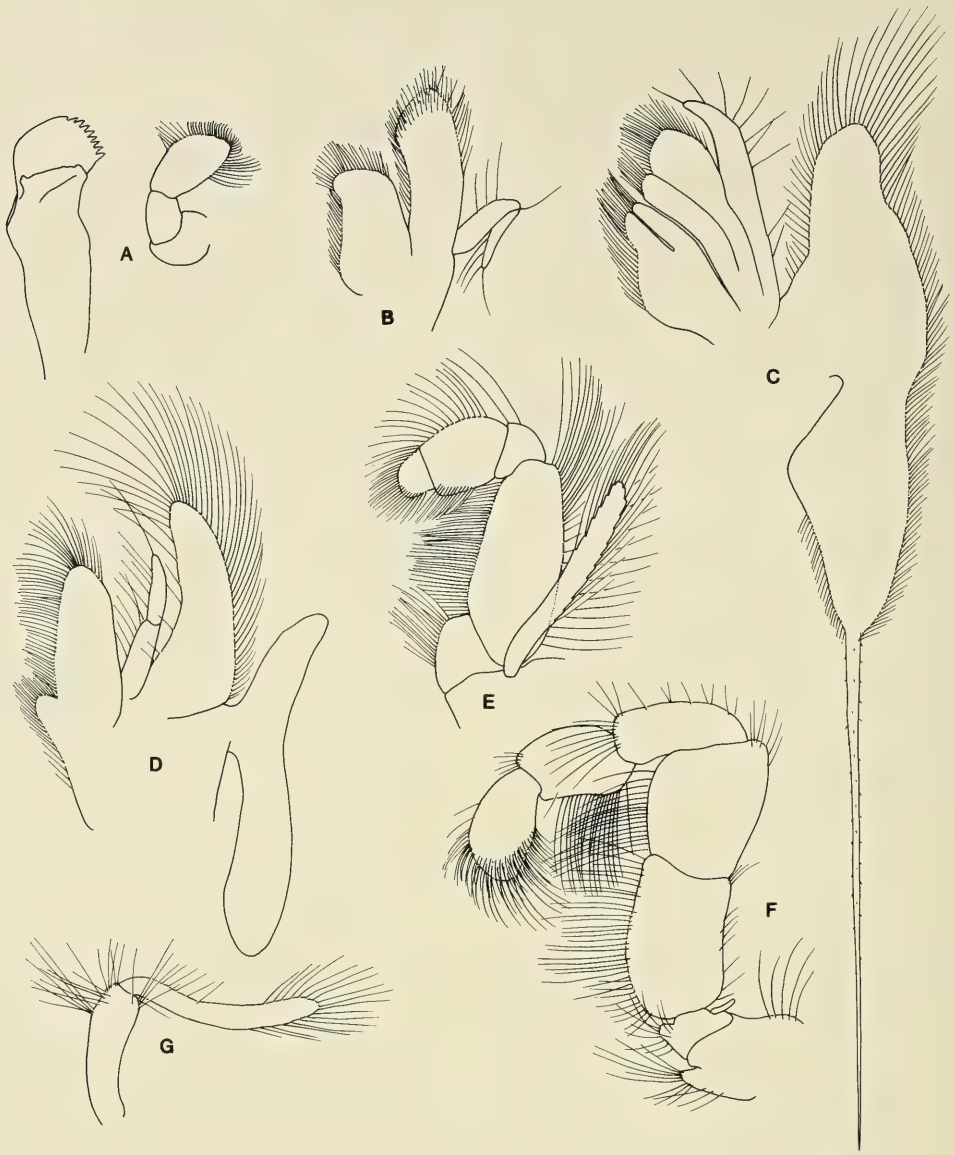


Fig. 23. *Mictaxius thalassicola*: A, Mandible with palp detached; B, Maxilla 1; C, Maxilla 2; D, Maxilliped 1; E, Maxilliped 2; F, Maxilliped 3; G, Pleopod 1, female.

1832) and *C. mucronata* Kossman, 1880, both appear to be synonyms of *Callianidea typa*.) How these taxa are related was investigated using PAUP (Swofford, 1985), a cladistic program that derives minimum-length trees based on the principle of parsimony, from which phylogeny may be inferred. Twenty-one morphological characters were used in this analysis.

The characters and character-states used are as follows (0 = plesiomorphic state; 1, 2, 3 = apomorphic states):

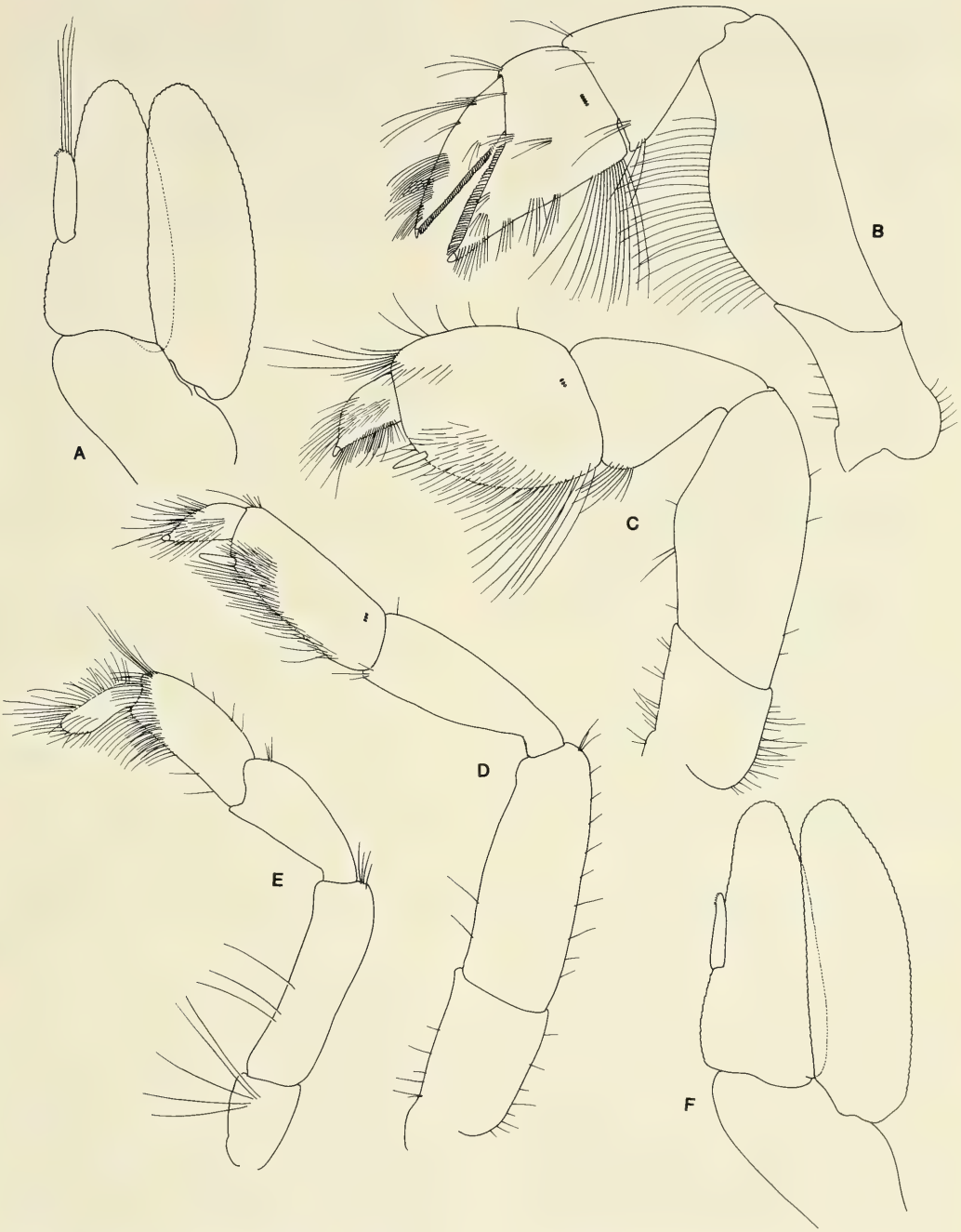


Fig. 24. *Mictaxius thalassicola*: A, Pleopod 2, male; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Pereopod 5; F, Pleopod 3.

1. Pereopod 1 chelipeds subsimilar (0), or strikingly dissimilar (1).

   The condition in *Callianidea* where in both sexes, the chelipeds of pereopod 1 are strongly unequal and dissimilar, implies a specialized separate function for each member of the pair of legs, with the one enlarged cheliped perhaps playing a role in agonistic or mating behavior.
2. Linea thalassinica present (1), or absent (0) [unordered].

   There is some uncertainty about whether the linea thalassinica is a primitive or advanced feature, and indeed, whether the linea thalassinica is an homologous structure in the various thalassinideans in which it occurs. Its presence in the callianassids, generally considered to be highly specialized burrowing forms, would suggest that at least in some groups the linea thalassinica is an advanced feature.
3. Pleopodal accessory respiratory filaments absent (0), or present (1).

   Development of these supposedly supplementary respiratory structures may have allowed the invasion of habitats characterized by fine sediments and somewhat restricted water flow, as under large intertidal beachrock slabs or in burrows in fine anoxic sediments. Increasing the surface area of the pleopods, which are in more direct contact with oxygen-bearing water than are the gills within the gill-chamber, would allow more effective gas exchange. The possibility of clogging of the gill chamber with fine sediment particles then becomes less critical for respiration.
4. Antennal acicle spiciform (0), or reduced to a small, often immobile scale (1).

   In the more specialized burrowing thalassinideans such as the callianassids, the antennal acicle is reduced to the point of being absent.
5. Maxilla 2, scaphognathite whip present (0), or absent (1).

   This would be a constant character in the analysis with *Callianassa* deleted, but for *Jaxea* (which has 5–7 elongate whips) which is coded as 9 (= unknown or not applicable).
6. Eye normal, i.e., with cornea delimited and well pigmented (0), or with cornea indistinct and reduced pigmentation (1).

   Along with the reduction of pigment, flattening of the eyestalk is seen in several different crustacean groups and is frequently correlated with a burrowing habit.
7. Maxilliped 2, exopod well developed (0), or reduced (1).
8. Maxilliped 3, exopod well developed (0), or reduced or lacking (1).
9. Lateral ramus of uropod distally entire (0), or bilobed (1).

   A bilobed lateral uropodal ramus has generally been regarded as characteristic of the more advanced callianassid genera (de Saint Laurent 1973).
10. Lateral ramus of uropod having a transverse suture (0), or lacking a suture (1).
11. Propodi of pereopods 3 and 4 unspecialized and subcylindrical (0), or broadened and flattened (1).
12. Mandibular incisor entire or with one or two low cusps (0), or toothed (1).
13. Setal rows on abdominal somites absent (0), or present (1).
14. Setal rows on pereopods 2, 3, and 4 absent (0), or present (1).
15. Epipods on pereopods 1–4 present (0), or absent (1).
16. Pleopod 2 in male unmodified (0), or modified (1).
17. Pleonite 1 with anteriorly-directed lobes (0), or lacking lobes (1).

   The submedian posterodorsal lobes of the carapace fit beneath the anterodorsal lobed part of the first pleuron; simultaneously, the posteromedian convexity of the carapace slides over the anteromedian part of the first abdominal somite. This combination, found in all the axiids, prevents dorsalventral and lateral overextension of

the abdomen, and only functions if the exoskeleton is strongly sclerotized. As thalassinideans become more specialized for permanent burrow or tunnel life, hardened exoskeletons become less necessary, and this interlocking of carapace and abdomen is lost.

18. Setal row pattern (0), (1), (2) [unordered].
19. Pereopod 1 meral pattern (0), (1) [unordered].

    The posterior margin of the merus of pereopod 1 is either convex, with or without one or more low serrations (pattern 0), or the posterior margin is straight, with one (rarely 2) strong marginal tooth (pattern 1).
20. Maxilliped 3, ischial crest present (0), or absent (1).
21. Pleopodal respiratory filaments rounded (0), or flattened (1) [unordered].

The data matrix used in the analysis is presented in the Appendix.

Results of PAUP Analysis
Fig. 25

Three genera, each from a different thalassinidean family, were chosen to serve as the outgroup for comparison with the eight taxa forming the ingroup: *Axiopsis* (family Axiidae), *Jaxea* (family Laomediidae), and *Callianassa* (family Callianassidae).

When *Callianassa* was included in the analysis as part of the outgroup, the ingroup could not be rooted as monophyletic and the resultant trees were then rooted at the midpoint. With *Callianassa* as part of the ingroup, it was joined with *Thomassinia* to form a sister group to the *Crosniera-Mictaxius* group. As noted above *Mictaxius* in particular possesses features thought to be more characteristic of the Callianassidae; this group thus seems to stand in a position transitional to the Callianassidae. *Callianassa* was thus omitted from the final analyses, making characters 15 and 16 constant for the rest of the taxa.

With *Callianassa* deleted from the analysis, and characters 2, 18, and 21 unordered, three trees were produced, each of length 25.00, and having a consistency index of 0.760.

The three trees differ only in the configuration of the taxa *Mictaxius, Thomassinia* and *Crosniera,* each of the trees having one of the three possible combinations for these three taxa (other than the possibility of an unresolved trichotomy).

Four apomorphic characters define the ingroup: (10) loss of a uropodal suture; (11) broadening of the propodi of pereopods 3 and 4; (13) setal rows present on the carapace and abdomen; (14) setal rows present on the propodi of pereopods 2–4.

The ingroup consists of two sister-groups: 1, the *Michelea-Marcusiaxius-Meticonaxius* group, defined by three characters, viz. loss of a linea thalassinica, acquisition of setal pattern 0, and meral pattern 1 for pereopod 1; 2, the *Callianidea-Crosniera-Mixtaxius-Thomassinia* group, defined by four characters, viz. reduction of the antennal acicle, toothed mandibular incisor, loss of somite 1 articulating lobes, non-flattened pleopodal respiratory filaments.

Further examination of character changes in the trees suggests the following:

Character 2: The linea thalassinica has been lost, in the *Michelea-Meticonaxius-Marcusiaxius* group, as well as in *Callianidea typa.*

Character 3: Pleopodal respiratory filaments have been acquired independently in two groups, i.e., in *Callianidea,* and in *Michelea.*

Character 8: The exopod of maxilliped 3 has twice been reduced or lost, in the *Crosniera-Mictaxius-Thomassinia* group and in the *Marcusiaxius-Meticonaxius* group.

Character 14: Setal rows on the pereopods have been lost in *Crosniera.*

Character 18: The setal row pattern of the *Michelea-Marcusiaxius-Meticonaxius* group, as well as that of the *Crosniera-Mictaxius-Thomassinia* group, have been

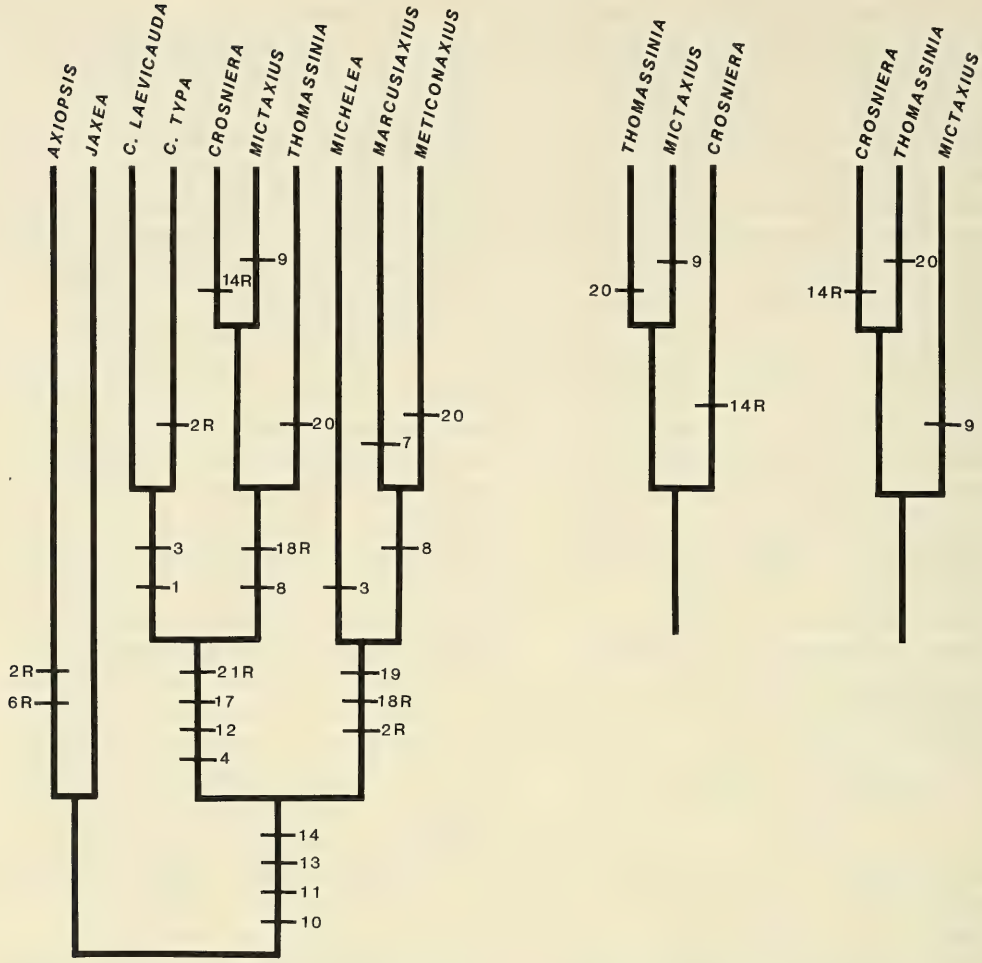


Fig. 25. Cladograms resulting from PAUP analysis of 22 characters and 11 taxa. Numbers refer to characters listed in text. Outgroup = *Axiopsis-Jaxea.* Changes in character-states indicated by bars. R = presumed character reversal.

derived from that of the *C. laevicauda-typa* group.

Character 20: The dentate ischial crest of maxilliped 3 has twice been lost, once in *Thomassinia,* and again in *Meticonaxius.*

Acknowledgments

We thank L. Watling of the University of Maine, R. B. Manning of the Smithsonian Institution, and A. B. Williams of the National Marine Fisheries Service, for a critical reading an early draft of the manuscript and for their useful comments. We are grateful to Dr. Torben Wolff of the Zoological Museum, Copenhagen, Ms. Ardis Johnston of the Museum of Comparative Zoology, Harvard University, Ms. Michelle van der Merwe of the South African Museum, Cape Town, and Dr. D. Platvoet of the Zoological Museum, Amsterdam, for the loan of material. Dr. Gary Poore of the Victoria Museum, Melbourne, and Dr. Michèle de Saint Laurent, of the Paris Museum provided details of their work on the thalassinideans, including some of their illustrations, and frequently shared ideas and

insights that had escaped us. For this generosity we are extremely grateful.

Literature Cited

Balss, H. 1925. Macrura der Deutschen Tiefsee-Expedition. 1. Palinura, Astacura und Thalassinidea.—Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899, 20(4):189–216.

———. 1957. Decapoda.—Dr. H. G. Bronn's Klassen und Ordnungen des Tierreichs, 5, Abteilung 1, Buch 7, Lieferung 12:1505–1672.

Barnard, K. H. 1950. Descriptive catalogue of South African decapod Crustacea (crabs and shrimps).—Annals of the South African Museum 38:1–837.

Bate, C. S. 1888. Report on the Crustacea Macrura collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76, Zoology 24:i–xc, 1–942.

Boas, J. E. V. 1880. Studier over Decapodernes Slaegtskabsforhold.—Dansk Videnskabernes Selskab, Copenhagen, Skrifter, series 6, naturvidenskabelig og mathematisek Afdeling 1(2):23–210. [Mémoires de l'Académie Royal de Copenhague, 1885, series 6, Classe des Sciences 1(2): 1–188.]

Borradaile, L. A. 1903. On the classification of the Thalassinidea.—Annals and Magazine of Natural History (7)12:534–551.

Bouvier, E. L. 1905. Sur les Thalassinides recueillis par le Blake dans la mer Antilles et le golfe du Mexique.—Compte Rendus de Séances de l'Académie des Sciences, Paris, 141(31):802–806.

———. 1925. Reports on the results of dredging under the supervision of Alexander Agassiz in the Gulf of Mexico (1877–78), in the Caribbean Sea (1878–79), and along the Atlantic coast of the United States (1880), by the U.S. Coast Survey Steamer "Blake," Lieut.-Com. C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. 48. Les Macroures Marcheurs.—Memoirs of the Museum of Comparative Zoology at Harvard College 47(5):399–472.

Carvalho, H. A. de, & S. de A. Rodrigues. 1973. *Marcusiaxius lemoscastroi,* g. n., sp. n., nova ocorrencia de familia Axiidae (Crustacea, Decapoda, Thalassinidea) no Brasil.—Boletim de Zoologia e Biologia Marinha, São Paulo, N. S. 30:553–566.

Coelho, P. A. 1973. Descriçao preliminar de *Meticonaxius minutus,* n. sp. do Norte do Brasil (Crust., Decapoda, Axiidae).—Ciencia e Cultura 25(6) supplement:345.

———. 1987. Uma espécie nova de *Meticonaxius* do Brasil (Crustacea, Decapoda, Callianeidae).—Revista Brasileira de Zoologia, São Paulo 4(1): 63–69.

———, & M. Ramos-Porto. 1987. Sinopse dos crustaceos decapodos Brasileiros (Familias Callianassidae, Callianideidae, Upogebiidae, Parapaguridae, Paguridae, Diogenidae).—Trabalhos Oceanograficos, Universidade Federal de Pernambuco 19:27–53.

———, ———, & M. L. Koening. 1980. Biogeografia e bionomia dos crustaceos do litoral equatorial Brasileiro.—Trabalhos Oceanograficos, Universidade Federal de Pernambuco 15:7–138

Gill, T. 1859. Descriptions of a new species of *Callianidea* Ed.—Proceedings of the Philadelphia Academy of Sciences 1859:167–168.

Gore, R. H. 1987. *Callianidea vandoverae* species nova (Decapoda, Thalassinidea, Callianideidae) from off the central eastern Florida coast, U.S.A.—Crustaceana 53(2):186–194.

Guérin-Méneville, F. E. 1829–1844. Crustacés, [1844] pp. 6–48, *in* Iconographie du Regne Animal de G. Cuvier, ou répresentation d'après nature de l'une des espèces les plus remarquables et souvent non figurées de chaque genre d'animaux. Avec un texte descriptif mis au courant de la science. Ouvrage pouvant servir d'atlas a tous les traités de zoologie. Paris and London, J. B. Baillière.

Gurney, R. 1938. Larvae of decapod Crustacea. Part 5. Nephropsidea and Thalassinidea.—Discovery Reports 17:291–344.

International Commission on Zoological Nomenclature, 1989. Opinion 1522. *Callianidea* H. Milne Edwards, 1837 (Crustacea, Decapoda): conserved.—Bulletin of Zoological Nomenclature 46(1):61–62.

Kensley, B. 1981. On the zoogeography of southern African decapod Crustacea, with a distributional checklist of the species.—Smithsonian Contributions to Zoology 338:1–64.

———. 1989. New genera in the thalassinidean families Calocarididae and Axiidae (Crustacea: Decapoda).—Proceedings of the Biological Society of Washington 102:960–967.

———, & R. Heard. 1990. The genus *Axianassa* (Crustacea: Decapoda: Thalassinidea) in the Western Atlantic and Eastern Pacific.—Proceedings of the Biological Society of Washington 103:558–572.

Kossmann, R. 1880. Reise in die Kustengebiete des Rothen Meeres, volume 2, part 1, section III, Malacostraca.—Zoologische Ergebnisse einer im Aufträge der koniglichen Academie der Wissenschaften zu Berlin 1880:67–140.

Le Loeuff, P., & A. Intes. 1974. Les Thalassinidea (Crustacea, Decapoda) du Golfe de Guinee. Sys-

tematique - Ecologie.—Cahiers ORSTOM 12(1): 17–69.

Man, J. G. de. 1905. Diagnoses of new species of macrurous decapod Crustacea from the "Siboga-Expedition."—Tijdschrift der Nederlandsche Dierkundige Vereeniging (2)9(3/4):587–614.

———. 1925. The Decapoda of the Siboga-Expedition. Part VI. The Axiidae collected by the Siboga-Expedition.—Siboga Expeditie Monographie 39a5:1–127.

———. 1928. The Decapoda of the Siboga-Expedition. Part 7. The Thalassinidae and Callianassidae collected by the Siboga-Expedition with some remarks on the Laomediidae.—Siboga Expeditie Monographie 39a6:1–187.

Manning, R. B. 1987. Notes on western Atlantic Callianassidae (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington, 100(2):386–401.

Melin, G. 1939. Paguriden und Galatheiden von Prof. Dr. Sixten Bocks Expedition nach den Bonin-Inseln 1914.—Kungliga Svenska Vetenskapsakademiens Handlingar, series 3, 18(2):1–119.

Milne Edwards, H. 1837. Histoire naturelle des Crustacés, Comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux, vol. 2, 532 pp. Paris: Librairie Encyclopédique de Roret.

Poore, G. C. B., & D. J. G. Griffin. 1979. The Thalassinidea (Crustacea: Decapoda) of Australia.—Records of the Australian Museum 32(6):217–321.

Rathbun, M. J. 1901. The Brachyura and Macrura of Porto Rico.—Bulletin of the U. S. Fish Commission for 1900 2:1–137.

Rodrigues, S. 1983. Aspectos da Biologia de Thalassanidea do Atlantico Tropical Americano. Doctoral thesis, University of São Paulo, 174 pp.

———, & H. A. de Carvalho. 1972. *Marcusiaxius lemoscastroi,* g.n., sp. n., primeira occurrencia da familia Axiidae (Crustacea, Decapoda, Thalassinidea) no Brasil.—Ciencia e Cultura, Supl. 24(6):357.

Saint Laurent, M. de. 1973. Sur la systématique et la phylogénie des Thalassinidea: définition des familles des Callianassidae et des Upogebiidae et diagnose de cinq genres nouveaux (Crustacea Decapoda).—Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris, series D, 277:513–516.

———. 1979. Sur la classification et la phylogénie des Thalassinides: définitions de la superfamille des Axioidea, de la sous-famille des Thomassiniinae et de deux genres nouveaux (Crustacea Decapoda).—Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris, series D, 288:1395–1397.

Sakai, K. 1987. Two new Thalassinidea (Crustacea: Decapoda) from Japan, with the biogeographical distribution of the Japanese Thalassinidea.—Bulletin of Marine Science 41(2):296–308.

———, & L. B. Holthuis. 1987. *Callianidea* H. Milne Edwards, 1837 (Crustacea, Decapoda): proposed conservation.—Bulletin of Zoological Nomenclature 44(2):92–94.

———, & M. de Saint Laurent. 1989. A check list of Axiidae (Decapoda, Crustacea, Thalassinidea, Anomura), with remarks and in addition descriptions of one new subfamily, eleven new genera and two new species.—Naturalists 3:1–104.

Schmitt, W. L. 1924. Bijdragen tot de kennis der fauna van Curaçao. Resultaten eener reis van Dr. C. J. van der Horst in 1920. The macruran, anomuran and stomatopod Crustacea.—Bijdragen tot de Dierkunde 23:61–81.

———. 1935. Crustacea Macrura and Anomura of Porto Rico and the Virgin Islands.—Scientific Survey of Porto Rico and the Virgin Islands, New York Academy of Sciences 15(2):125–227.

———. 1936. Zoologische Ergebnisse einer Reise nach Bonaire, Curaçao und Aruba im Jahre 1930. No. 16. Macruran and Anomuran Crustacea from Bonaire, Curaçao and Aruba.—Zoologische Jahrbucher, Abteilung für Systematik, Ökologie und Geographie der Tiere 67(5/6):363–378.

——— 1939. Decapod and other Crustacea collected on the Presidential Cruise of 1938 (with introduction and station data).—Smithsonian Miscellaneous Collections 98(6):1–29.

Stebbing, T. R. R. 1920. South African Crustacea.—Annals of the South African Museum 17(4):231–272.

Swofford, D. L. 1985. PAUP: phylogenetic analysis using parsimony, user's manual, Illinois Natural History Survey.

(BK) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (RWH) Gulf Coast Research Lab, P.O. Box 7000, Ocean Springs, Mississippi 39564-7000.

Appendix.—Data matrix used in present analysis.

Taxa	Characters
Axiopsis	*00000000000000009009
Callianassa	*11011111111001119019
Jaxea	*01009100000000009009
C. laevicauda	11110100011111012000
C. typa	10110100011111012000
Michelea	00100100011011010101
Crosniera	01010101011110011009
Mictaxius	01010101111111011009
Thomassinia	01010101011111019019
Marcusiaxius	00000111011011000109
Meticonaxius	00000101011011000119

* = Outgroup.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 538–544

REEXAMINATION OF THE TYPE MATERIAL OF *MUNIDA MILITARIS* HENDERSON, 1885 (CRUSTACEA: DECAPODA: GALATHEIDAE), WITH THE SELECTION OF A LECTOTYPE

Keiji Baba and Enrique Macpherson

Abstract.—The type material of *Munida militaris* Henderson, 1885, has been found to contain three species: *Munida militaris, M. japonica* Stimpson, 1858, and *M. inornata* Henderson, 1885. In order to clarify the taxonomy of *Munida militaris* Henderson, 1885, a lectotype is selected from "Challenger" Station 173 off Matuku, Fiji Islands, and a description of Henderson's original type material is provided.

Based upon the *Challenger* material, Henderson (1885:410) described *Munida militaris* from four different localities (Stations 173, 192, 200 and Ambon) without listing specimens. Henderson (1888:137), in his subsequent extensive account of the *Challenger* collection, synonymized *Munida vitiensis* Henderson, 1885, from Station 173, with *M. militaris,* although the original description of the former preceded that of the latter on the same page, and removed the locality record listed in his 1885 paper for *Munida militaris* from Station 200. The type of *M. vitiensis* could not be found in the collection in the Natural History Museum, London (formerly the British Museum (National History)) (BM). Very possibly it might have been combined with the type of *M. militaris* from Station 173 by Henderson himself.

As the type material of *Munida militaris* now comprises three species (*Munida militaris* Henderson, 1885, *M. japonica* Stimpson, 1858, and *M. inornata* Henderson, 1885) (Baba 1990:963), there is the need to select a lectotype for *M. militaris,* and to describe it in detail. In the following account, the carapace length (cl) includes the rostrum.

There is another query about the identity of *Challenger* material of *Munida militaris curvirostris* Henderson, 1888 [originally *M. militaris* var. *curvirostris*]. Henderson (1885: 412) described *M. curvirostris* from Station 210, but it was transferred under *M. militaris* as a variety (in the sense of a subspecies) in the 1888 paper, in which he listed a male from Station 200, in addition to a female (holotype of *M. curvirostris*) from Station 210. In all probability the Station 200 specimen may be the one that Henderson (1888:138) removed from the list of material of *M. militaris* (see above). Recently, Baba (1988:81) who briefly revised the genus *Munida* and provided a key to the Indo-West Pacific species of the genus, synonymized Henderson's variety (subspecies) with *M. militaris.* However, examination of the material of *M. militaris curvirostris* (BM 1888:33) disclosed that it is distinct from *M. militaris* and identical with *M. andamanica* Alcock, 1894, which is a well-known species in the Indo-West Pacific. This conclusion was drawn by comparison both with one of the *Investigator* materials (male, cl = 29.5 mm) taken in the Andaman Sea in 173 fm (317 m) and now deposited in the Smithsonian Institution (USNM 19017), and, more specifically, with 16 specimens from nine different localities in the Philippines and Indonesia made available from the Zoological Museum, Copenhagen (Baba,

unpublished data), of *M. andamanica*. The details will be incorporated in Baba's report still in progress on the collection of the *Galathea* Expedition.

Munida militaris Henderson, 1885
Fig. 1

Munida militaris Henderson, 1885:410 (part); 1888:137 (part), pl. 14: figs. 2, 2a, 2b, 5, 5a, 5b.—Baba, 1988:85 (key).
Munida vitiensis Henderson, 1885:410.

Type material.—*Challenger* Sta 173 off Matuku, Fiji Islands, 576 m (315 fm): 2 ♂ (cl = 9.5, 21.9 mm), 2 ovig. ♀ (cl = 16.6, 17.0 mm) [Larger male is selected as lectotype (BM 1888:33)].—Ambon, Indonesia, 183 m (100 fm): 1 ♂ (cl = 19.8 mm).

Description.—Carapace excluding rostrum slightly longer than wide, epigastric region with transverse row of spines, consisting usually of 8 spines in 4 pairs, first pair (mesial) small, second pair (closest to mesial one) largest and situated directly behind supraocular spines, third and fourth pairs (lateral) small, occasionally with additional 1–2 spines lateral to each; lateral protogastric spine on each side; anterior branchial region with small spine directly behind midlength of anterior bifurcation of cervical groove. Front margin feebly oblique. Lateral margin of carapace usually with 7 spines, anterior 2 situated in front of cervical groove, first anterolateral, strong, directed nearly straight forward or slightly oblique, second occasionally accompanied by spinule in front of and/or behind it; remaining 5 (rarely 6) present on anterior branchial region. No spine on posterior ridge.

Rostrum nearly horizontal or weakly upcurved, barely half as long as remaining carapace. Supraocular spines about half length of rostrum, directed slightly laterad.

Second abdominal segment with row of 8–10 dorsal spines.

Eyes dilated, corneas 0.3 times as wide as long, setae short.

Basal antennular segment overreaching cornea, with 2 terminal subequal spines. Antennal peduncle having first (proximal) segment with stout mesial distoventral spine reaching about to end of second segment; second segment with 2 terminal spines; distomesial spine well developed, occasionally overreaching end of peduncle.

Merus of third maxilliped with 2 spines (occasionally with tiny process or spine equidistant between them) on flexor margin, proximal prominent, distal small and terminal; distodorsal margin unarmed; ischium with 26–32 denticles on mesial ridge.

Chelipeds spinose, with iridescent and plumose setae. Meri relatively short, stout; dorsal surface with 2 rows of spines and few scattered spinules on distal portion; lateral margin with moderate-sized distal spine followed by denticles or small denticular spines proximal to it; mesial margin with 2 or 3 spines in distal half, distal spine stouter but of moderate size; ventral surface with 2 spines (one spine well developed, situated near distomesial margin, another spine small, distal in midline). Carpi with 2 rows of spines dorsally, lateral row occasionally obsolete; with 4 or 5 spines mesially, proximal one tiny and somewhat dorsal, median 2 well developed (second one from distal end more so), distal one small. Palm twice as long as wide, dorsally with 2 rows of small spines: middle row with 2 accompanying spines (one spine distal, another spine proximal), another row of spines near mesial margin, occasionally with few spines; mesial surface with 2 rows of spines: one dorsal, consisting of 3–4 spines and other ventral, consisting of 2 or 3 spines, accompanied by 1–3 small spines further ventral to it; laterally with 4–7 spines continued into margin of fixed finger. Fingers as long as, or slightly longer than palm, terminating in curved claws (crossed when closed), opposable margins slightly gaping or not; movable finger with proximal marginal spine rarely

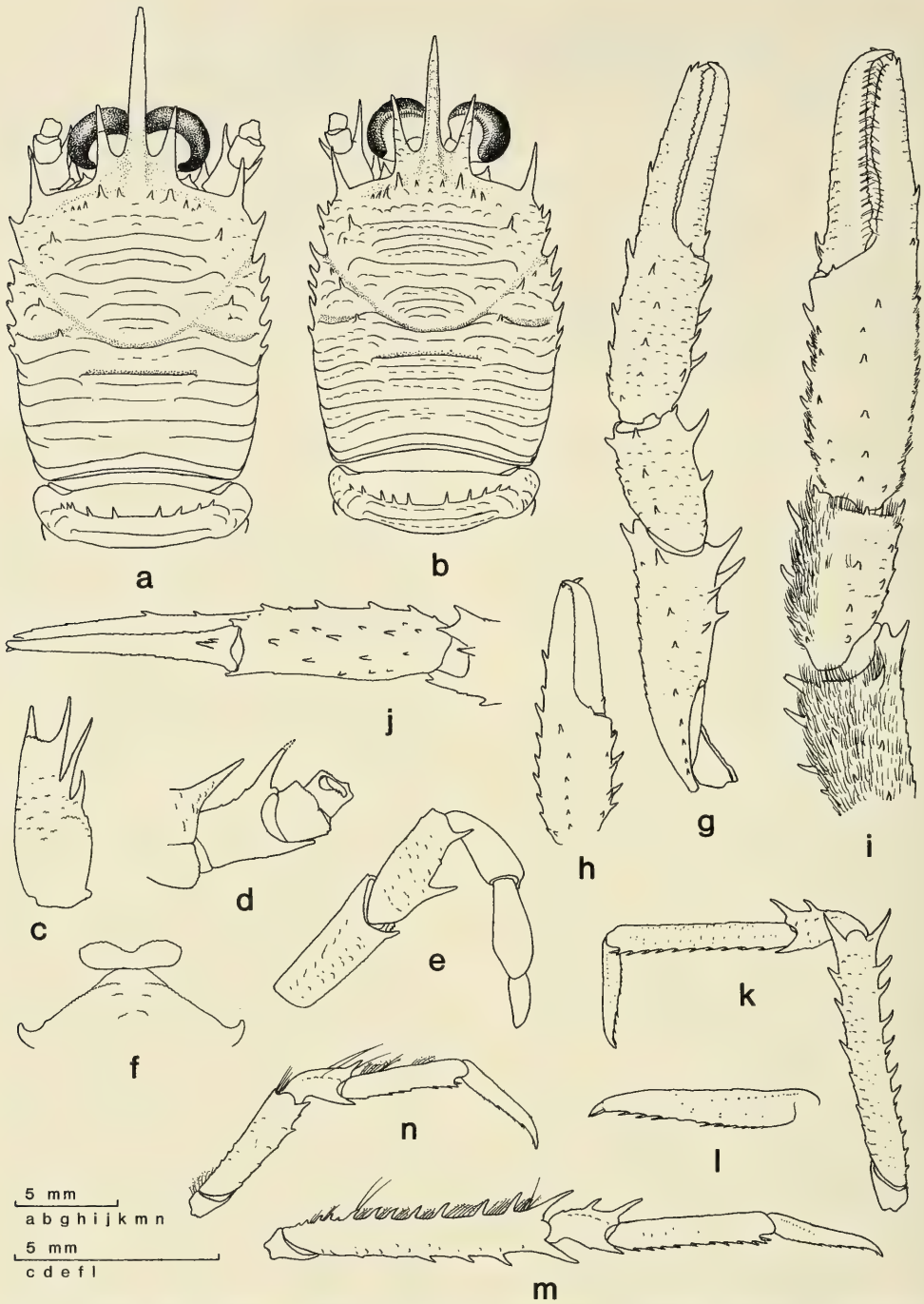


Fig. 1. *Munida militaris* Henderson, 1885: a, c–h, k, l, types from "Challenger" Station 173 off Matuku, Fiji Islands. a, c, d–f: male lectotype, g, h, k, l: detached appendages from type specimens, b, i, j, m, n: paralectotype male from Ambon. a, b, carapace and anterior part of abdomen; c, basal segment of left antennule, ventral view; d, left antennal peduncle, ventral view; e, endopod of right third maxilliped; f, anterior part of sternum; g, left cheliped; h, left chela (granulation omitted); i, right cheliped; j, chela of same, lateral view; k, left first or second walking leg (largest among detached walking legs); l, dactylus of same; m, right first walking leg; n, right third walking leg.

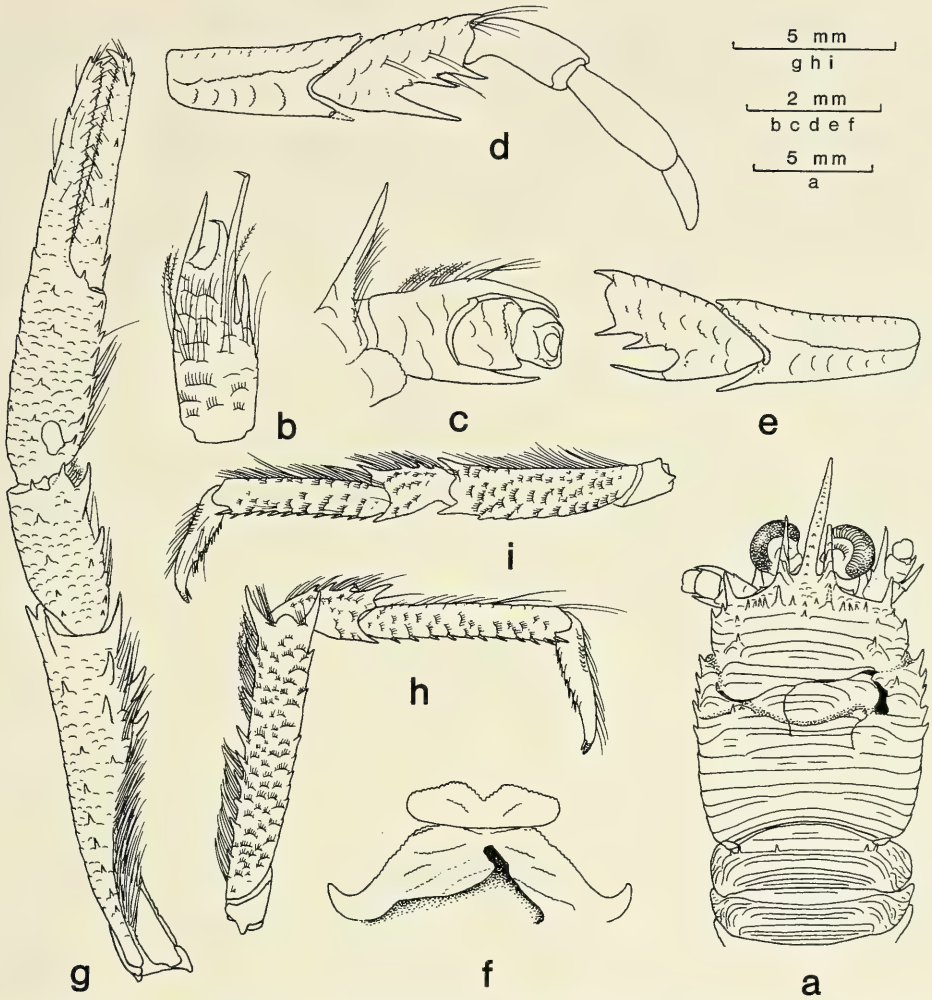


Fig. 2. *Munida japonica* Stimpson, 1858, female from *Challenger* Station 173 off Matuku, Fiji Islands, cl 15.0 mm [originally one of the syntypes of *M. militaris* (see Henderson 1885:411, 1888:138)]. a, carapace and anterior part of abdomen; b, basal segment of left antennule, ventral view; c, left antennal peduncle, ventral view; d, endopod of right third maxilliped; e, merus and ischium of left third maxilliped; f, anterior part of sternum; g, left cheliped; h, right first or second walking leg; i, left third walking leg.

accompanied by dorsal spinule; fixed finger with 3 or 4 lateral marginal spines, distal 2 at base of curved terminal claw.

Meri of first and second walking legs with 11–13 dorsal and 4–5 ventral spines, each terminal spine prominent; carpi with 2 prominent terminal and 1 or 2 moderate-sized dorsal spines; propodi 6–7 times as long as wide, with about 11 ventral movable spinules (distal 2 paired, mesial one of them invisible in lateral view); dactyli distinctly more than half length of propodi, distally with somewhat curved claw preceded by 10–13 low processes and movable spinules on ventral margin. Third walking leg shortest, merus in particular; merus with very minute dorsal spines; carpus unarmed except distodorsal spine; propodus with about 8 movable, slender ventral spines.

Male with 2 pairs of pleopods modified as gonopods.

Remarks.—One lot from *Challenger* Station 173 off Matuku, Fiji Islands (Henderson, 1888:138) contains five specimens (2

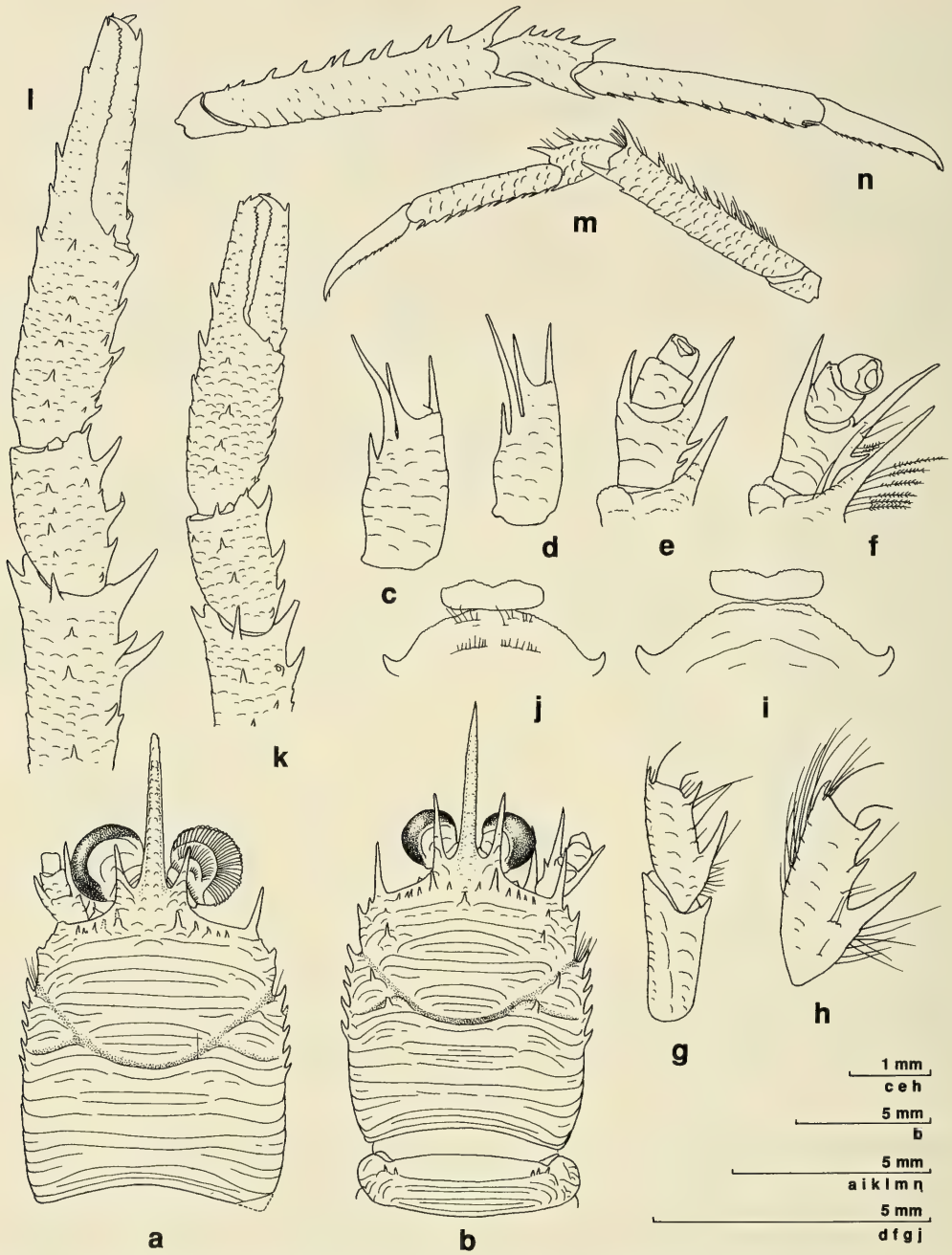


Fig. 3. *Munida inornata* Henderson, 1885 (a, c, e, g, i, k, n), and *M. japonica* Stimpson, 1858 (b, d, f, h, j, l, m) from *Challenger* Station 192 off Little Ki Island [originally syntypes of *M. militaris* (see Henderson 1885: 411, 1888:138)]. a, carapace; b, carapace and anterior part of abdomen; c, d, basal segment of right antennule, ventral view; e, f, right antennal peduncle, ventral view; g, proximal 2 segments of endopod of right third maxilliped, lateral view; h, merus of right third maxilliped; i, j, anterior part of sternum; k, l, left cheliped, dorsal view (proximal part omitted); m, left first or second walking leg, lateral view; n, right first or second walking leg, lateral view.

♂, 2 ovig. ♀, 1 ♀), one of which, the nonvigorous female (cl = 7.6 mm), represents *Munida japonica* Stimpson, 1858 (see Fig. 2). All pereopods were found detached in this lot, of which one set of appendages in our opinion belong to *M. japonica* based primarily on their very scaly condition. However, the true identity of this specimen is unclear. Variations observed in Philippine specimens (Baba 1988:109), as well as material from Japan, Taiwan, Eastern Australia, New Caledonia and Madagascar (Baba & Macpherson, unpublished data), suggest the existence of a *M. japonica* complex, which includes two or more species.

The male from Ambon (Henderson 1888: 138) (Fig. 1b, i, j, m, n) generally agrees with the specimens from Station 173, only differing in that the carapace has many more secondary striae and the branchial region with one or two additional spinules along the anterior bifurcation of the cervical groove, the cheliped is more setose, and has slightly gaping fingers. These differences, however, seem to have no systematic importance.

Two females in a lot from *Challenger* Station 192 off Little Ki Island, Indonesia (see Henderson 1888:138), are not referable to *M. militaris*. In fact, Henderson (1888:138) noted abnormalities of these specimens in the longer rostrum, the smooth and glabrous carapace with several spinules, the short and slim chelipeds, and the second abdominal segment provided with very obsolete spinules. Examination of the syntypes of *M. inornata* (BM 1888:33) has allowed us to confirm that the smaller specimen (cl = 11.5 mm) represents *M. inornata* Henderson, 1885 (Fig. 3a, c, e, g, i, k, n); the supraocular spines are very short, barely one-third the length of the rostrum, the lateral protogastric and postcervical spines as well as the anterior branchial spines along the anterior bifurcation of the cervical groove are absent, and the second segment of the antennal peduncle bears two mesial marginal spines, in addition to the strong terminal one, as defined earlier for the Philippine specimen of *M. inornata* (Baba 1988: 106). The only difference we found between the present material and the syntypes of *M. inornata* is that the smaller of the mesial marginal spines of the second antennal segment is absent in the latter. The larger ovigerous female (cl = 16.0 mm) displays characters of *M. japonica* as noted above for the specimen from Station 192 (Fig. 3b, d, f, h, j, l, m). This lot also contains a small detached cheliped and a third left maxilliped which apparently belong to another unknown species.

Henderson's (1888) figure 5 of Plate 14 incorrectly depicts the epigastric spination. Figure 2 of that plate is no doubt illustrated from one of the specimens from off Matuku. In order to clarify the taxonomy of *M. militaris,* and to retrict the type locality, the larger male from *Challenger* Station 173 off Matuku is selected as the lectotype for Henderson's species.

Munida militaris strongly resembles *M. benguela* de Saint Laurent & Macpherson, 1988, originally known from the South African coast between southern Namibia and Natal, and subsequently from Madagascar; their relationships are discussed in Baba (1990:963).

Acknowledgments

We thank R. W. Ingle and Paul Clark for loaning the type materials of *Munida militaris* and *M. curvirostris,* and for working space and facilities during a visit of one of us (EM) to the Natural History Museum, London, 1989. We are also indebted to R. B. Manning and R. Lemaitre, both of the Smithsonian Institution, A. L. Rice of the Institute of Oceanographic Sciences, Surrey, and an anonymous reviewer, for critical reading of the manuscript.

Literature Cited

Alcock, A. 1894. Natural history notes from H.M. Indian Marine Survey Steamer "Investigator,"

commander R.F. Hoskyn, R.N., late commanding. Series II, No. 1. On the results of the deep-sea dredging during the season 1890–91 (continued).—Annals and Magazine of Natural History, Series 6, 13:321–334.

Baba, K. 1988. Chirostylid and galatheid crustaceans (Decapoda: Anomura) of the "Albatross" Philippine Expedition, 1907–1910.—Researches on Crustacea, The Carcinological Society of Japan, Special Number 2: v + 203 pp.

———. 1990. Chirostylid and galatheid crustaceans of Madagascar (Decapoda, Anomura).—Bulletin du Muséum national d'Histoire naturelle, Paris, Série 4, Section A, (1989) 11(4):921–975.

Henderson, J. R. 1885. Diagnoses of the new species of Galatheidea collected during the "Challenger" Expedition.—Annals and Magazine of Natural History, Series 5, 16:407–421.

———. 1988. Report on the Anomura collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873–76, Zoology, 27:vi + 221 pp., 21 pls.

Saint Laurent, M. de, & E. Macpherson. 1988. *Munida benguela,* espèce nouvelle d'Afrique du Sud. Comparaison avec *Munida sanctipauli* Henderson, 1885 (Crustacea Decapoda Galatheidae).—Bulletin du Muséum national d'Histoire naturelle, Paris, Série 4, Section A, 10(1):105–115.

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VII. Crustacea Anomura.—Proceedings of the Academy of Natural Sciences of Philadelphia, 10:225–252.

(KB) Faculty of Education, Kumamoto University, Kurokami 2-40-1, 860 Japan; (EM) Instituto de Ciencias del Mar, Consejo Superior de Investigaciones Cientificas, Paseo Nacional s/n 08003 Barcelona, Spain.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 545–555

TWO SIMILAR SPECIES: *PLESIONIKA EDWARDSII* (BRANDT, 1851) AND *PLESIONIKA CROSNIERI*, NEW SPECIES (CRUSTACEA: DECAPODA: PANDALIDAE)

Tin-Yam Chan and Hsiang-Ping Yu

Abstract.—Two species previously confounded under the name *Plesionika edwardsii* (Brandt, 1851) are recognized from the Indo-Pacific region, one bearing more than one post-rostral tooth is also found in the Mediterranean and Atlantic, while the other with only a single post-rostral tooth is known only from the Indo-Pacific. Although the type of *P. edwardsii* probably cannot be now verified, the type locality is selected as the Mediterranean. A reexamination of the syntypes of *P. longirostris* (Borradaile, 1900) from New Britain proved that it is a junior synonym of *P. edwardsii.* The Indo-Pacific species with only a single post-rostral tooth is described as new, with a holotype selected from Taiwanese material. The differences between the two species are discussed and their coloration illustrated.

In the older literature, *Plesionika edwardsii* (Brandt, 1851) was confused with *Plesionika narval* (Fabricius, 1787) (e.g., de Man 1920, Dieuzeide 1931). This was mainly because the beautiful illustration provided by H. Milne Edwards (1841, pl. 54, fig. 2) of *Pandalus narval* actually portrays a species different from that of Fabricius (1787). Brandt (1851) cast doubt on the identity of H. Milne Edwards' figure and proposed the name *Pandalus* (*Pontophilus*) *Edwardsii* for the specimens illustrated. However, both H. Milne Edwards (1841) and Brandt (1851) did not indicate the locality of the specimen, though the species had subsequently been widely reported in the Mediterranean and Atlantic (Crosnier & Forest 1973). In 1900, Borradaile described a closely related species *Pandalus* (*Parapandalus*) *longirostris* from New Britain but in his report he did not mention *P. edwardsii* nor *P. narval* at all. In later literature, the name *P. edwardsii* is always applied to material from the Mediterranean and Atlantic (e.g., Zariquiey Alvarez 1968, Pequegnat 1970, Crosnier & Forest 1973, Holthuis 1980), while that from the Indo-Pacific was called *P. longirostris* (e.g., Stebbing 1914; Barnard 1950; Crosnier & Jouannic 1973; Crosnier 1976; Suzuki 1974; King, 1981, 1984).

Recently, Chace (1985) compared his limited *Albatross* Philippines material with those from the Atlantic (including the Mediterranean) and concluded that the different populations should be treated as the same species. However, when we examined the Taiwanese *P. edwardsii,* it was found that the material displays two forms of coloration. It also appears that several slight but constant differences are always associated with the difference in coloration. A later visit to European museums by the first author revealed that the two forms are widely distributed (though not always together) in the Indo-Pacific but that only one is present in the Mediterranean and the Atlantic. Although the type of *P. edwardsii* cannot be verified from H. Milne Edwards' material deposited in the Muséum National d'Histoire Naturelle, Paris, its type locality is determined to be in the Mediterranean. A reexamination of the syntypes of *P. longirostris* showed that they belong to the same species

as those from the Mediterranean. Therefore, *P. longirostris* is synonymized with *P. edwardsii* but with reason very different from that proposed by Chace (1985). The species which is found only in the Indo-Pacific and not in the Mediterranean is then considered as new and described in detail. The differences between these two species are discussed and their coloration illustrated.

Specimens labeled NTOU remain deposited at the National Taiwan Ocean University, USNM at the National Museum of Natural History, Washington D.C., MNHN at the Muséum National d'Histoire Naturelle, Paris, RMNH at the Rijksmuseum van Natuurlijke Historie, Leiden, UMZC at the University Museum of Zoology, Cambridge. The measurement listed in mm under "Material examined" is the carapace length, measured dorsally from the post-orbital margin to the posterior margin of the carapace.

Plesionika crosnieri, new species
Figs. 1, 3a

Plesionika longirostris.—Stebbing, 1914:37 (in part).—Barnard, 1950:681, fig. 126n.—Crosnier & Jouannic, 1973:11, pl. 2, fig. 2 (in part ?).—Suzuki, 1974:27, fig. 1b–e.—Crosnier, 1976:234 (in part).—Kensley, 1981:28.—King, 1984:182, fig. 6 (in part ?); 1987:193, figs. 2 & 5 (in part?) [non Borradaile, 1900].

Plesionika edwardsii.—Chace, 1985:62 (in part), fig. 26a–e [non Brandt, 1851].

Material examined.—Holotype: Ta-Chi, I-Lan County, northeastern Taiwan, fish market, "baby" shrimp trawler, 19 Jun 1990: 1 ovig. ♀ 21 mm, NTOU. Paratypes (all at NTOU): Fish markets, "baby" shrimp trawlers, Ta-Chi, I-Lan County, 9 Dec 1984: 1 ovig. ♀ 24 mm; 8 May 1985: 1 ♂ 23 mm, 1 ovig. ♀ 24.5 mm; 14 May 1988: 2 ♂♂ 20, 22.5 mm, 2 ovig. ♀♀ 21, 21.5 mm; 28 Apr 1989: 2 ♂♂ 18, 22 mm, 2 ovig. ♀♀ 18, 21 mm; 20 Sep 1990: 2 ovig. ♀♀ 21, 23.5 mm. Tong-Kong, Ping-Tong County, about 130 m, 19 Jan 1989: 6 ♂♂ 11–21 mm, 6 ovig. ♀♀ 18–23 mm, 1 ♀ 18 mm. Southern coast, R.V. *Hai-Kung,* 22°01′N, 120°35′E, 350 m, traps, 30 Oct 1987: 1 ♀ 17.5 mm. Other specimens (not paratypes): Japan, Sagami Bay, H. Suzuki coll., 6 May 1973: 2 spec; 23 Jun 1973: 1 spec, RMNH. Crozet Islands, MD08, Stn 7, CC48: 5 spec, MNHN.

Description.—Rostrum curved downwards basally, then strongly curved upwards (nearly straight) beyond antennular peduncle, and occasionally bending slightly downwards again near apex; far overreaching scaphocerite, 1.8–2.5 ($\bar{X}$ = 2.2) times as long as carapace; dorsal border armed with 16–29 ($\bar{X}$ = 24) teeth over entire length, anterior teeth closely set but posterior ones larger and spaced farther apart, ventral border bearing 30–43 ($\bar{X}$ = 36) closely packed teeth on upturned section. Post-rostral carina slightly elevated and bearing single fixed tooth, which is always smaller than posteriormost dorsal rostral tooth (very rarely almost at level of post-orbital margin), and with small posterior notch. Distance between post-rostral tooth and posteriormost dorsal rostral tooth equal to or slightly greater than that between posterior two dorsal rostral teeth. Eye large and subspherical, with distinct ocellus. Orbital margin regularly concave. Antennal and pterygostomian spines well developed. Stylocerite sharply acute with outer margin narrow and curved very slightly upwards, reaching to about middle of second antennular segment. Scaphocerite with distolateral tooth reaching nearly or quite to distal margin. Basicerite spine well developed and sharp, extending nearly to proximal end of outer scaphocerite margin.

Maxilliped 3, with distal two segments subequal, bearing rudimentary epipod and extending to about distal margin of scaphocerite. Four anterior pereiopods with reduced epipods, those of pereiopods 1 and 2 minute and inconspicuous while those at pereiopods 3, 4 small but distinct. Pereiopods 1 and 2 reaching to distal margin of

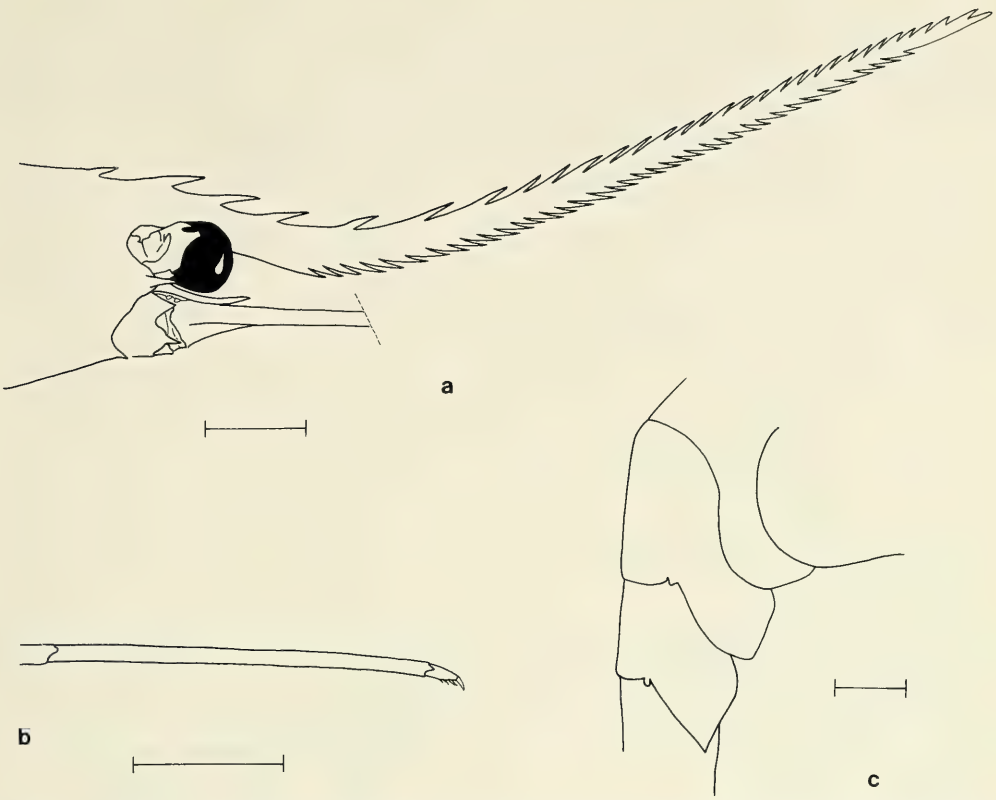


Fig. 1. *Plesionika crosnieri,* new species. Holotype, ovigerous female, cl = 21 mm, Ta-Chi, I-Lan County, Taiwan. a, lateral view of anterior carapace and rostrum. b, distal two segments of right pereiopod 3. c, lateral view of abdominal somites 3 to 5. Scales = 5 mm.

scaphocerite, pereiopods 2 subequal and having 19–27 ($\bar{X}$ = 22) carpal articles. Posterior 3 pereiopods moderately stout, with propodi shorter than carapace, dactyl very short. Pereiopod 3 overreaching scaphocerite by small fraction of carpus, pereiopod 4 by more or less than length of propodus, and pereiopod 5 by about ½ length of propodus. Dactylus of pereiopod 3 about $\frac{1}{10}$ as long as propodus, that of pereiopod 4 about $\frac{1}{15}$, and of pereiopod 5 about $\frac{1}{18}$.

Dorsal surface of abdominal somites 1 and 2 rounded, those of posterior somites slightly arched (especially at somite 3) but not sharply angular. Pleura of anterior four somites rounded but pleuron 5 bearing sharp denticle postero-ventrally. Telson more or less as long as abdominal somite 6, usually armed with 3 pairs of dorso-lateral spinules and 3 pairs of terminal spines. Eggs oval and numerous, about 0.5 mm in diameter.

Coloration.—Body pale pink. Eyes black brown. Upturned section of rostrum red. Carapace uniformly colored, only with orbital margin and ventral parts somewhat reddish. Organs inside carapace vermilion and/or greenish blue, sometimes dorsally also with pair of iridescent yellowish green lines. Antennal and antennular flagella pinkish orange, pereiopods pink. Mouth parts, distal segment of maxilliped 3 and pereiopod 1, reddish. Abdomen with about 11 (13 in ovigerous females) somewhat faint longitudinal red stripes; dorsal midline bearing single red stripe extending to posterior margin of somite 3, dorsal second and

Table 1.—Major differences between *Plesionika edwardsii* (Brandt, 1851) and *P. crosnieri*, new species.

	P. edwardsii (Brandt, 1851)	*P. crosnieri*, new species
Post-rostral tooth	2–4, posteriormost typically minute, variably movable and abutting against or close to 2nd tooth	single fixed tooth far from posteriormost dorsal rostral tooth
Rostral teeth	27–36 on dorsal border, 37–52 on ventral border	16–29 on dorsal border, 30–43 on ventral border
Stylocerite	outer margin broad and distinctly curved upwards	outer margin narrow and only very slightly curved upwards
Basicerite spine	often slightly overreaching proximal end of scaphocerite margin	always failing to reach proximal end of scaphocerite margin
Coloration	generally strong; carapace with faint white stars and posterior vertical white band*, abdomen with stripes deeply colored and dorsal midline covered with pair of submedian stripes, distal end of uropods with iridescent yellowish white patches*	generally pale; carapace without white spots or bands, abdomen with stripes faint and dorsal midline covered with single stripe, distal end of uropods not particularly marked

* But quickly disappeared with becoming less fresh.

third stripes fused at posterior end of somite 4. Abdominal hinges distinctly reddish. No iridescent markings at uropods. Eggs bright blue, becoming dirty white when near hatching.

Type locality.—Taiwan.

Distribution.—Indo-West-Pacific and Southern Ocean, but so far only known with certainty from the eastern coast of South Africa, La Réunion, Crozet Islands, Indonesia, Philippines, Taiwan, Japan and New Caledonia (see Remarks). At depths of 80–350 m.

Remarks.—The new species is extremely similar to *P. edwardsii*. Except for plentiful fresh material available in Taiwan we would probably have not been able to recognize the difference between the two species. When the two species occur together in the same catch they can be readily distinguished by the different coloration. Furthermore, such color difference is always associated with several morphological differences as listed in Table 1. A reexamination of Chace's (1985) *Albatross* material of *P. edwardsii* showed that the two species were confounded. Chace's female from Indonesia (fig. 26a) has only one fixed post-rostral tooth, while the other two from the Philippines have two or three post-rostral teeth (with the posteriormost apparently movable). Examinations of the numerous specimens deposited at MNHN and RMNH showed that the two species are widely distributed in the Indo-Pacific, and available photographs always show the different coloration. However, all the material from the Mediterranean and Atlantic bear more than one post-rostral tooth and is apparently identical with the redder form from the Indo-Pacific.

There was no indication of the locality for the specimen illustrated as *Pandalus narval* (not *Astacus Narval* Fabricius, 1787) by H. Milne Edwards (1841, pl. 54, fig. 2). Brandt (1851) also had not specified the type locality of *P. edwardsii*. Although H. Milne Edwards' figure shows only one post-rostral tooth on the carapace, that tooth is nearly at the level of the post-orbital margin, a situation that seems very unlikely. In the collection of the MNHN, there is only one lot of specimens labeled as "*Pandalus narval,* Naples, ancienne collection" by H. Milne Edwards. There are three specimens in this lot; one being the true *P. narval* while the other two are "*P. edwardsii*." The latter two are ovigerous females (19 and 22.5 mm cl), and in very poor condition (rostrum

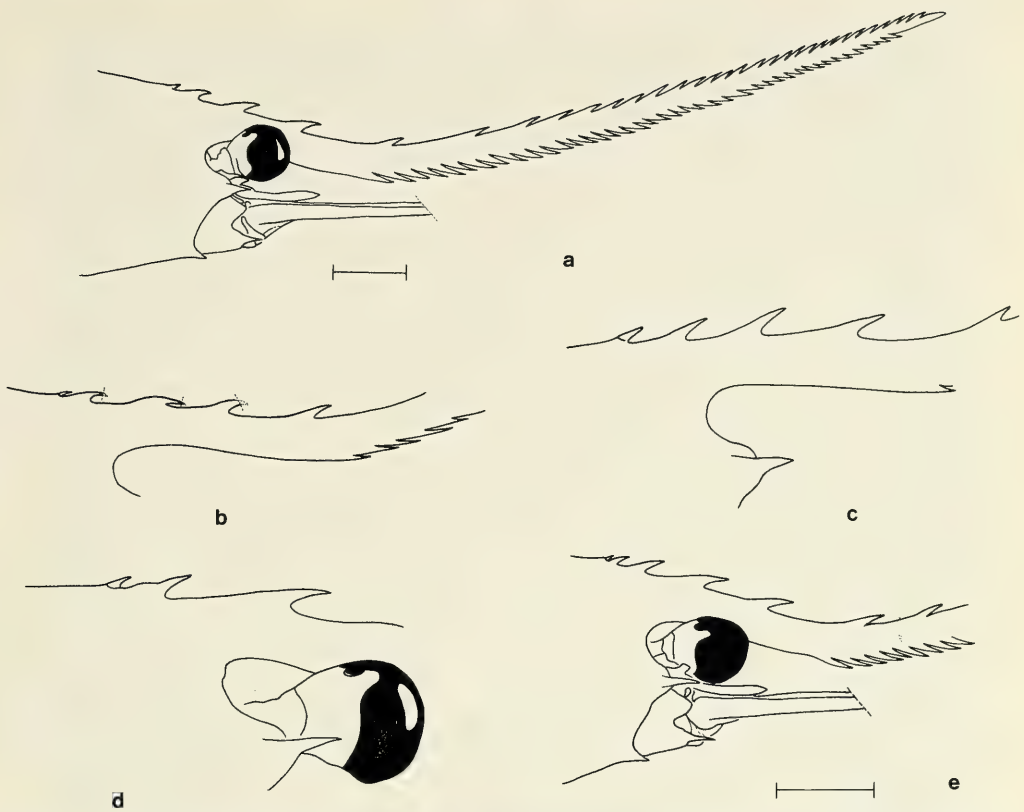


Fig. 2. *Plesionika edwardsii* (Brandt, 1851). a, lateral view of anterior carapace and rostrum, ovigerous female cl = 24.5 mm, from Sicily, off Pantellerid Island. b–e, lateral view of anterior carapace: b, ovigerous female cl = 22.5 mm from Naples, identified by H. Milne Edwards as *Pandalus narval*; c, ovigerous female cl = 18 mm, syntype of *P. longirostris* (Borradaile, 1900); d, female cl = 20 mm, syntype of *P. longirostris*; e, ovigerous female cl = 21.5 mm from Ta-Chi, I-Lan County, Taiwan. Scales = 5 mm.

broken). Although the larger female is similar in size to the one figured by H. Milne Edwards (1841), no eggs are shown in the figure and both specimens have two postrostral teeth on the carapace (fig. 2b). Thus, either the specimen illustrated by H. Milne Edwards was from the Indo-Pacific and accurately drawn or it was from the Mediterranean and poorly drawn.

Based on the available information, we conclude that the possibility that H. Milne Edwards' figure was drawn from a specimen collected in the Indo-Pacific is very unlikely. This is because species mentioned by H. Milne Edwards from the Indo-Pacific were mostly, if not all, from shallow water. *Pandalus edwardsii* is a deep-water species and, in H. Milne Edwards' days, deep-water material almost always came from the Mediterranean. Although difficult to prove, the specimen illustrated was probably from the Mediterranean and inaccurately drawn (i.e., the minute posteriormost movable postrostral tooth overlooked). Thus, the type locality of *P. edwardsii* is believed to be in the Mediterranean. It is, however, still not certain that the two females identified as *Pandalus narval* by H. Milne Edwards in MNHN should be treated as the types. Yet, this conclusion leaves no alternative but to identify the form with more than one postrostral teeth as *P. edwardsii*.

The remaining problem is whether the other species could represent *P. longirostris,* described by Borradaile (1900) from New Britain. Borradaile's figure (1900, pl. 37, fig. 10a) clearly shows only one post-rostral tooth present on the carapace but in the text he stated that there were from three to four teeth of the rostral series located on the carapace. However, the descriptions and illustrations provided by Borradaile (1900) are generally considered to be inaccurate (e.g., Stebbing 1914, Chace 1985). The types examined of *P. longirostris* from UMZC contain two badly damaged females (18 and 20 mm cl, rostrum broken), the smaller one being ovigerous. Both specimens have two post-rostral teeth on the carapace with the posteriormost movable (fig. 2c, d) and are in other respects similar to the Mediterranean *P. edwardsii.* Thus, *P. longirostris* should be synonymized with *P. edwardsii.* The material with only one fixed post-rostral tooth, even though resembling both H. Milne Edwards' and Borradaile's figures, actually is of an undescribed species.

Examination of the material deposited at MNHN and RMNH showed that, in addition to Taiwan, the two species occur sympatrically in New Caledonia, La Réunion, Indonesia and the Philippines. So far, only *P. crosnieri* has been found in Japan and Crozet Island (hundreds of additional specimens in the MNHN from this Southern Ocean locality are probably all *P. crosnieri*). On the other hand, only *P. edwardsii* is found in the Mediterranean and the Atlantic and at New Britain, Fiji, French Polynesia in the Indo-Pacific. From other reports, both or either of the species are also present in Madagascar (Crosnier & Jouannic 1973), Seychelles (Crosnier, unpublished photo), Marianas, Samoa, Tonga and Hawaii (King 1984, 1987). For Vanuatu, the photographs illustrated in King (1981, as *P. longirostris*) clearly show the typical coloration of *P. edwardsii.* Although Chace (1985) expressed doubt about the exact identity of the small specimens reported as *P. longirostris* from South Africa by Stebbing (1914) and Barnard (1950), the descriptions and figure provided by the latter author closely resemble *P. crosnieri,* with the shorter telson likely due to the very small size of the specimens. It will be of interest to have more data on the distribution of these two species.

Etymology.—The species is named after Dr. A. Crosnier for his invaluable help in furnishing us the definitive information (i.e., finding H. Milne Edwards' material and reexamining Borradaile's types) that finally established the status of this species.

Plesonika edwardsii (Brandt, 1851)
Figs. 2, 3b

Pandalus narval.—H. Milne Edwards, 1841: pl. 54, fig. 2 [not *P. narval* (Fabricius, 1787)].

Pandalus (Pontophilus) Edwardsii Brandt 1851:122 [type locality (herein designated): Mediterranean].

Pandalus (*Parapandalus*) *longirostris* Borradaile, 1900:413, pl. 37, fig. 10a–h [type locality: New Britain].

Plesionika longirostris.—de Man, 1920: 114—Crosnier & Jouannic, 1973:11, pl. 2, fig. 2 (in part ?).—Crosnier, 1976:234 (in part), fig. 4a.—King, 1981:14, figs. 6–7, 2 unnumbered photo; 1984:182 (in part ?), fig. 4-Pl, fig. 6 (in part ?); 1987:193, figs. 2 & 5 (in part ?).

Parapandalus Narwal.—de Man, 1920:138 [not *P. narval* (Fabricius, 1787)].

Pandalus narwal.—Dieuzeide, 1931:3, figs. 1–4, 1 unnumbered pl. [not *P. narval* (Fabricius, 1787)].

Plesionika edwardsii.—Zariquiey Alvarez, 1968:109, fig. 45.—Pequegnat, 1970:93.—Crosnier & Forest, 1973:202, figs. 63b, 64b.—Holthuis, 1980:144.—1987:251, unnumbered figs.—Chace, 1985:62 (in part), fig. 26f–g.

not *Plesionika edwardsii.*—Takeda, 1983: 62, unnumbered photo [= ?].—Chace, 1985:62 (in part), fig. 26a–e [= *P. crosnieri,* new species].

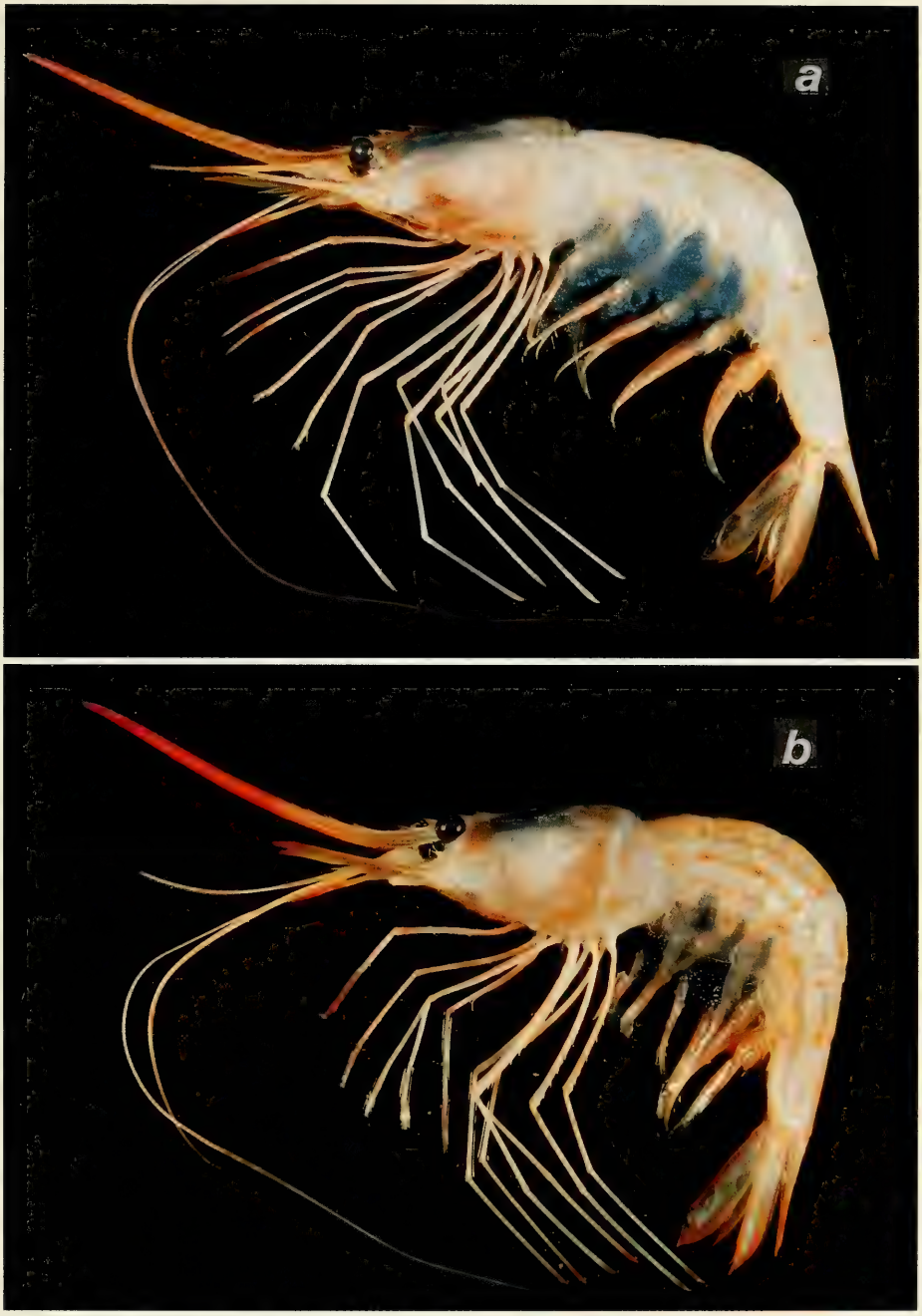


Fig. 3. a, *Plesionika crosnieri,* new species: ovigerous female, cl = 23.5 mm, Taiwan; b, *Plesionika edwardsii* (Brandt, 1851): ovigerous female, cl = 24 mm, Taiwan.

not *Plesionika longirostris.*—Stebbing, 1914: 37 (in part).—Barnard, 1950:681, fig. 126n.—Crosnier & Jouannic, 1973:11, pl. 2, fig. 2 (in part ?).—Suzuki, 1974:27, fig. 1b–e.—Crosnier, 1976:234 (in part).—Kensley, 1981:28.—King, 1984:182, fig. 6 (in part ?); 1987:193, figs. 2, 5 (in part ?) [= *P. crosnieri,* new species].

Material examined.—Mediterranean: Italy, Naples, "ancienne collection," labeled *Pandalus narval* by H. Milne Edwards and in the same jar with one specimen of *P. narval* (Fabricius, 1787): 2 ovig. ♀♀ 19, 22.5 mm, MNHN (? larger specimen illustrated in pl. 54, fig. 2 in H. Milne Edwards 1841); Sicily, off Pantellerid Island, Luiciotta, 36°14′12″N–36°14′30″N, 12°18′06″E–12°15′30″E, 400 m, 21 Jun 1974: 4 ♂♂ 14–21 mm, 1 ovig. ♀ 24.5 mm, NTOU (USNM exchange). Nice, France, NA2060, labeled *Parapandalus narval* by A. Milne-Edwards: 1 ovig. ♀ 25.5 mm, MNHN. Barcelona, Spain: 5 spec, RMNH; 300 m, 6 Jun 1956: 2 spec, RMNH; 5 Aug 1961: 1 ovig. ♀ 26 mm, RMNH. Algeria, Jun 1927: 2 spec, RMNH. NW Atlantic: Norfolk Canyon, *Gilliss* Stn 76-01, 37°01′30″N, 74°00′39″W, 150 m, 31 Jan 1976: 1 ♂ 19 mm, 1 ovig. ♀ 19.5 mm, NTOU (USNM exchange). Taiwan (all at NTOU): Fish markets, "baby" shrimp trawlers. Ta-Chi, I-Lan County, 4 Jun 1988: 1 ♂ 22.5 mm, 2 ovig. ♀♀ 24, 28.5 mm; 22 Jun 1989: 1 ovig. ♀ 20 mm; 10 Mar 1990: 1 ovig. ♀ 21.5 mm; 20 Sep 1990: 1 ovig. ♀ 23 mm. Tong-Kong, Ping-Tong County, 19 Jan 1989: 1 ovig. ♀ 24 mm. New Britain: Syntypes of *Pandalus* (*Parapandalus*) *longirostris* Borradaile, 1900: 1 ♀ 20 mm, 1 ovig. ♀ 18 mm, UMZC (examined by A. Crosnier). Fiji: Suva, Laucala Bay, King coll., 1979: 3 spec, RMNH.

Diagnosis.—Rostrum curved downward in basal region, then strongly curved upwards beyond antennular peduncle, slightly more than 2 times as long as carapace; armed dorsally with 28–36 teeth over entire length, anterior teeth closely spaced, posterior teeth larger and well spaced, ventral border bearing 37–52 closely spaced teeth. Two to 3 (rarely 4) post-rostral teeth on carapace, posteriormost tooth typically minute or small, variably movable and abutting against (sometimes only near) second posterior tooth. Eye large and subspherical, with distinct ocellus. Orbital margin regularly concave. Outer margin of stylocerite broad and distinctly curved upwards. Basicerite spine long, often slightly overreaching proximal end of outer margin of scaphocerite. Epipod on maxilliped 3 rudimentary, those on anterior 4 pereiopods reduced and sometimes inconspicuous on pereipods 1 and 2. Distal two segments of maxilliped 3 subequal. Pereiopods 2 subequal, with 18–28 carpal articles. Posterior three pereiopods moderately stout, with pereiopod 3 overreaching scaphocerite by small part of carpus, dactylus about $1/10$ as long as propodus. Dorsal surface of abdominal somite 3 slightly arched but not sharply angular. Abdominal pleuron 4 rounded, pleuron 5 pointed. Telson nearly as long as abdominal somite 6. Eggs ovate, numerous, about 0.5 mm in diameter.

Coloration.—Body pinkish white. Carapace with numerous soft white spots and bearing vertical white band near posterior margin (both fading quickly when becoming less fresh). Upturned section of rostrum, ventral carapace and mouth parts reddish. Organ inside carapace vermilion and/or dark blue, sometimes dorsally also with pair of iridescent yellowish green lines. Eyes dark brown and orbital margin red. Antennal and antennular flagella pinkish orange. Pereiopods pink and with distal segment of maxilliped 3 and pereiopod 1 somewhat reddish. Abdomen provided with 5 (6 in ovigerous females) pairs of deep red longitudinal stripes; with pair of submedian stripes near dorsal midline and second dorsal stripe extending only to posterior margin of somite 2. Abdominal hinges reddish. Distal ends of uropods with iridescent yellowish white patches. Eggs blue.

Distribution. —Worldwide: Mediterranean, Atlantic (east coast to Angola and west coast from Virginia, U.S.A., to Gulf of Mexico) and Indo-Pacific. In Indo-Pacific known with certainty only from La Réunion, Indonesia, Philippines, Taiwan, New Britain, New Caledonia, Vanuatu, Fiji and French Polynesia. At depths of 50–680 m, commonly 200–400 m.

Remarks. —The material from the Indo-Pacific is virtually identical with that from the Mediterranean and the Atlantic. The determination that *P. edwardsii* is distributed in both the Atlantic and Indo-Pacific by Monod (1966, in Crosnier & Forest 1973), and Chace (1985), should be credited although the conclusions were based on very different reasons. Chace's (pers. comm.) examination of 129 Mediterranean and 68 NW Atlantic specimens deposited at USNM showed that these specimens usually bear two or less frequently, three post-rostral teeth on the carapace. Only in one specimen (from the Mediterranean), four post-rostral teeth were present, with the posteriormost two movable. Another specimen (also from the Mediterranean), has the second posteriormost tooth directly above the post-orbital margin and with the posteriormost tooth movable. Most of the remaining specimens have the posteriormost tooth variably movable (about 5% have it virtually immovable), minute or small and often abutting against the second posterior tooth (fig. 2a, b). Sometimes the posteriormost tooth is well-separated from the second posterior tooth but the distance between the posterior two post-rostral teeth is always distinctly shorter than that between the second and third (or the posteriormost dorsal rostral tooth) teeth (fig. 2d). A brief examination of the other *P. edwardsii* material from various localities deposited at MNHN and RMNH, as well as those from Taiwan, also showed such trend of variations (e.g., fig. 2c, e; see also Crosnier & Forest 1973:fig. 63b). Furthermore, the outer margin of the stylocerite is always broad and distinctly curved upward in *P. edwardsii.* It also appears that the rostral teeth are generally higher in *P. edwardsii* (see Zariquiey Alvarez 1968, Pequegnat 1970, Holthuis 1987) than those of *P. crosnieri* (see Suzuki 1974). Although the epipods on the pereiopods are also reduced in *P. edwardsii,* those on pereiopods 1 and 2 are often larger than those of *P. crosnieri* and sometimes they are even nearly as large as those of pereiopods 3 and 4.

The stars and reddish color of *P. edwardsii* appears to be very constant in the Indo-Pacific material [King 1981 (photo of *P. longirostris*), 1984:fig. 4-Pl; Crosnier, unpublished photo]. King (1981, 1984) even called it the "Stars and stripes shrimp". Although such a color pattern can readily distinguish *P. edwardsii* from the pale colored *P. crosnieri,* the stars and white band on the carapace fade very quickly when the specimen becomes less fresh and making it appear very similar to the latter.

Plesionika edwardsii is reported to be of commercial potential from the Mediterranean (Holthuis 1980, 1987), and Vanuatu (King 1981). This shrimp also appears to be rather common in many eastern Atlantic and Indo-Pacific localities (e.g., Crosnier & Forest 1973; Crosnier 1976; King 1984, 1987). The "*P. edwardsii*" specimens reported by Takeda (1983) from Suriname and French Guiana seem to represent a very different species since they have very long dactylus, pointed abdominal pleuron 4 and completely different arrangement of basal rostral teeth and coloration. An examination of the La Réunion material deposited at MNHN showed that in this region *P. edwardsii* is much more common than *P. crosnieri.* However, the opposite is true for the material in Taiwan where *P. crosnieri* is the most common species, although the two species were sometimes found together in the same catch. The two are among the largest *Plesionika* species in Taiwan and both are sometimes sold in fish markets at a price of about NT$50-100/kg (usually mixed with other *Plesionika* species) under the common

name of "Mother shrimp" (a name used locally for all *Plesionika* and *Heterocarpus* species) because they always carry brightly colored eggs.

Acknowledgments

Grateful acknowledgment is extended to F. A. Chace, Jr. (USNM) for his kind help and for re-examining his material, and discussing with us the status of the two species; L. B. Holthuis (RMNH) for discussing with us the type locality of *P. edwardsii*; A. Crosnier (MNHN) for his important assistance and warmest hospitality while the first author visited Paris. We also thank C. H. J. M. Fransen (RMNH) for allowing the first author to examine their collection; R. C. Preece (UMZC) for sending the syntypes of *P. longirostris* to A. Crosnier so that he could examine them for us; D. A. Lee, of the Taiwan Fisheries Research Institute for providing us with a *P. crosnieri* specimen; J. Y. Shy of our laboratory for inking the Figures; and the Ministère des Affaires Etrangerès, France, for providing a research grant to the first author to visit MNHN. The present report is a contribution from the research grant on the Decapod Crustacea of Taiwan supported by the National Science Council, R.O.C.

Literature Cited

Barnard, K. H. 1950. Descriptive catalogue of South African decapod crustacea.—Annals of the South African Museum 38:1–837.

Borradaile, L. A. 1900. On the Stomatopoda and Macrura brought by Dr. Willey from the South Seas. *In* A. Willey, Zoological results based on materials from New Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896 and 1897. 4:395–428, pls. 36–39. Cambridge University Press.

Brandt, F. 1851. Krebse. A. T. von Middendorff, Reise in den äussersten Norden und Osten Sibiriens während der Jahre 1843 und 1844 mit allerhochster Genehmigung auf Veranstaltung der Kaiserlichen Akademie der Wissenschaften zu St. Petersburg ausgefuhrt und in Verbindung mit vielen Gelehrten herausgegeben. 2(1):77–148, pls. 5, 6.

Chace, F. A., Jr. 1985. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907–1910, Part 3: Families Thalassocarididae and Pandalidae.—Smithsonian Contributions to Zoology 411:1–153.

Crosnier, A. 1976. Données sur les Crustacés décapodes capturés par M. Paul Gueze a l'île Réunion lors d'essais de Pêche en eau profonde.—Travaux et Documents ORSTOM 47:225–256.

———, & J. Forest. 1973. Les crevettes profondes de l'Atlantique oriental tropical.—Faune Tropicale (O.R.S.T.O.M.) 19:1–409.

———, & C. Jouannic. 1973. Note d'information sur les prospections de la pente continentale malgache effectuées par le N.O. Vauban.—Document scientifique Centre ORSTOM Nosy Be 42: 1–18.

Dieuzeide, R. 1931. Sur la répartition de deux *Pandalus* des côtes algériennes.—Bulletin des Travaux publiés par la Station d'Aquiculture et de Pêche de Castiglione année 1931(1):1–12.

Fabricius, J. C. 1787. Mantissa insectorum sistens eorum species nuper detectas adiectis Characteribus genericis, differentiis specificis, emendationibus, observationibus. 1:xx + 348 pp. Hafniae.

Holthuis, L. B. 1980. FAO species catalogue, Vol. 1. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries.—FAO Fisheries Synopsis, (125) Vol. 1:1–261.

———. 1987. Crevettes. *In* W. Fischer, M. Schneider, & M. L. Bauchot, eds., Fiches FAO d'identification des espèces pour les besoins de la pêche. (Révision 1.) Mediterranée et mer Noire. Zone de pêche 37. Vol. I. Végétaux et Invertébrés: 191–292, many unnumbered figs. Rome, FAO.

Kensley, B. 1981. On the zoogeography of Southern African decapod Crustacea, with a distributional checklist of the species.—Smithsonian Contributions to Zoology 338:1–64.

King, M. G. 1981. Deepwater shrimp resources in Vanuatu: a preliminary survey off Port Vila.—Marine Fisheries Review 43(12):10–17, 10 figs.

———. 1984. The species and depth distribution of deepwater caridean shrimps (Decapoda, Caridea) near some southwest Pacific islands.—Crustaceana 47:174–191.

———. 1987. Distribution and ecology of deep-water caridean shrimps (Crustacea; Natantia) near tropical Pacific islands.—Bulletin of Marine Science 41:192–203.

Man, J. G. de. 1920. The Decapoda of the Siboga expedition, IV: Families Pasiphaeidae, Stylodactylidae, Hoplophoridae, Nematocarcinidae, Thalassocaridae, Pandalidae, Psalidopodidae, Gnathophyllidae, Processidae, Glyphocrangonidae and Crangonidae.—Siboga-Expeditie (39a3): 1–318, 25 pls.

Milne Edwards, H. 1841. Les Crustacés. *In* G. Cuvier, Le Règne Animal, distribué d'après son organisation, pour servir de base a l'histoire naturelle des animaux, et d'introduction à l'anatomie comparée. ed. 4. 18:1–278, 80 pls., Paris.

Monod, Th. 1966. Crevettes et crabes de la côte occidentale d'Afrique.—Mémoires de l'Institut Fondamental d'Afrique Noire 77:103–234.

Pequegnat, L. H. 1970. Deep-sea caridean shrimps with description of six new species.—Texas A&M University Oceanographic Studies 1:59–123.

Stebbing, T. R. R. 1914. South African Crustacea, Part VII.—Annals of the South African Museum 15(1):1–55, 12 pls.

Suzuki, H. 1974. Preliminary report of two Pandalidae (Crustacea, Caridea) from Sagami Bay.—Science Reports of the Yokohama National University II 21:27–29.

Takeda, M. 1983. Crustaceans. *In* M. Takeda & T. Okutani, eds., Crustaceans and mollusks trawled off Suriname and French Guiana: 21–185. Japan Marine Fishery Resource Research Centre, Tokyo, 354 pp.

Zariquiey Alvarez, R. 1968. Crustáceos decápodos ibéricos.—Investigación Pesquera (Barcelona) 32:1–510.

Graduate School of Fisheries, National Taiwan Ocean University, Keelung, Taiwan, Republic of China.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 556–560

EUTRICHOCHELES PINDATYBA, A NEW AXIID SHRIMP (CRUSTACEA: DECAPODA: THALASSINIDEA) FROM BRAZIL

Sérgio de Almeida Rodrigues and Brian Kensley

Abstract.—A new species of axiid, *Eutrichocheles pindatyba,* is described from Santa Cruz, south-central Brazil. The species is characterized by possessing a laterally dentate rostrum, unarmed median and submedian carinae of the carapace, spinose ischia and meri and tuberculate propodi of the first pereopods.

The genus *Eutrichocheles* was erected by Wood Mason (1876), to accommodate *Cancer modestus* Herbst, 1796, and was thought to be a member of the Astacidae (= Nephropsidae) (see Holthuis 1986). Later, Chopra (1933) and Balss (1933) concluded that Herbst's species was in fact an axiid, probably an *Axiopsis* of the subgenus *Paraxiopsis.* Recent authors (e.g., Sakai & de Saint Laurent 1989) have abandoned de Man's (1925) axiid subgenera; *Paraxiopsis* is now regarded as a junior synonym of *Eutrichocheles* Wood Mason.

Five species of *Eutrichocheles* have been described, of which only *E. defensus* (Rathbun, 1901) is known from the western Atlantic. A new species is now described from the coast of Brazil, based on a single specimen collected at Santa Cruz, Estado do Espirito Santo. This specimen is deposited in the Museu de Zoologia da Universidade de São Paulo, Brazil.

Family Axiidae

Eutrichocheles pindatyba, new species

Figs. 1–16, Table 1

Material.—Holotype, MZUSP 10580, ♂ cl 10.0 mm, Santa Cruz, Espirito Santo, Brazil, 19°57′S, 40°08′W, intertidal, under stones, coll. M. L. Christoffersen, Mar 1979.

Description.—Carapace (Figs. 1, 2): integument smooth, naked; small marginal antennal tooth present; rostrum at lower level than gastric region, with 6 teeth on right side, 5 on left; median carina unarmed, sharply keeled near rostral base; submedian carina unarmed, moderately keeled, with single long seta posteriorly; lateral carina continuing from rostral margin, unarmed except for single strong anterior tooth, bearing few short setae posterior to anterior tooth. Abdominal pleura (Fig. 1): integument bearing few long setae; pleuron 1 ventrally narrowed; pleuron 2 broadly rounded, caridean-like; pleura 3–6 irregularly rounded, each with small denticle on anterolateral margin.

Antennal acicle small, bifurcate (Fig. 3). Mouthparts (Figs. 4–8) as figured. Maxilliped 3 (Figs. 9. 10), ischium with 5 teeth on posterior margin, dentate crest strong; merus with 9 teeth on posterior margin, increasing in size distally; carpus with single distal tooth on posterior margin; propodus and dactylus unarmed. Pereopod 1: larger chela (Fig. 11), ischium with 2 strong teeth and serrations on posterior margin; merus with single tooth on anterior margin distal to midlength, 5 strong teeth and serrations on posterior margin; carpus with serrate posterior margin; propodus with anterior and posterior margins serrate, former ending distally in low tooth, mesial and external surfaces tuberculate, palm 1.5 times longer than fingers, fixed finger with several low teeth on cutting edge; dactylus with cutting edge raised near midlength, bearing several

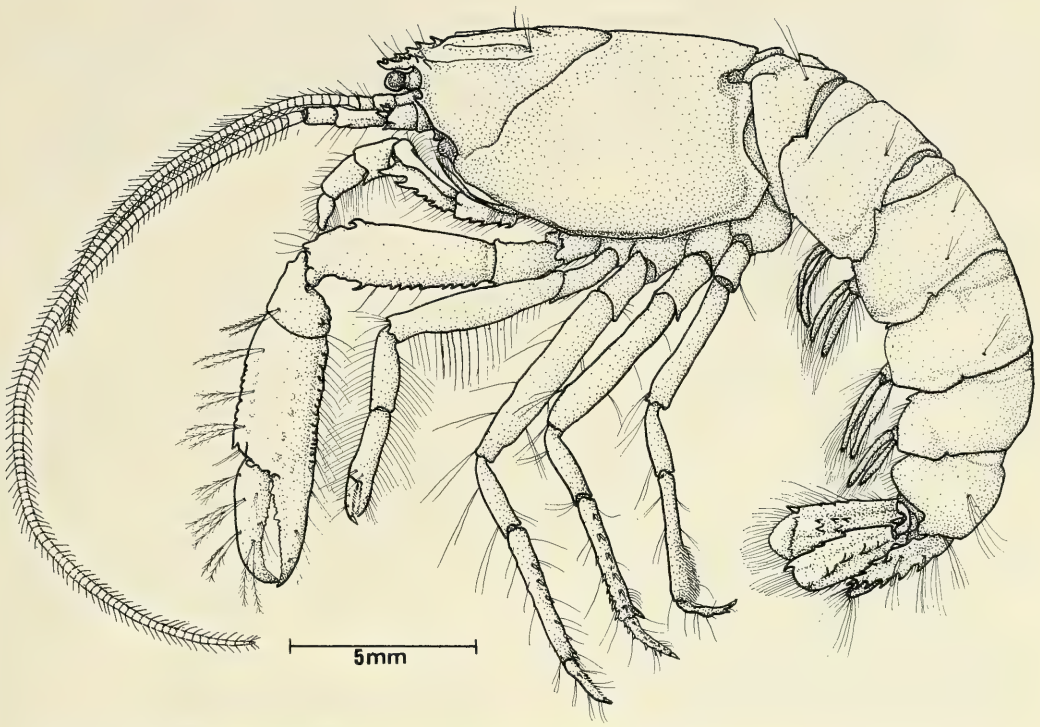
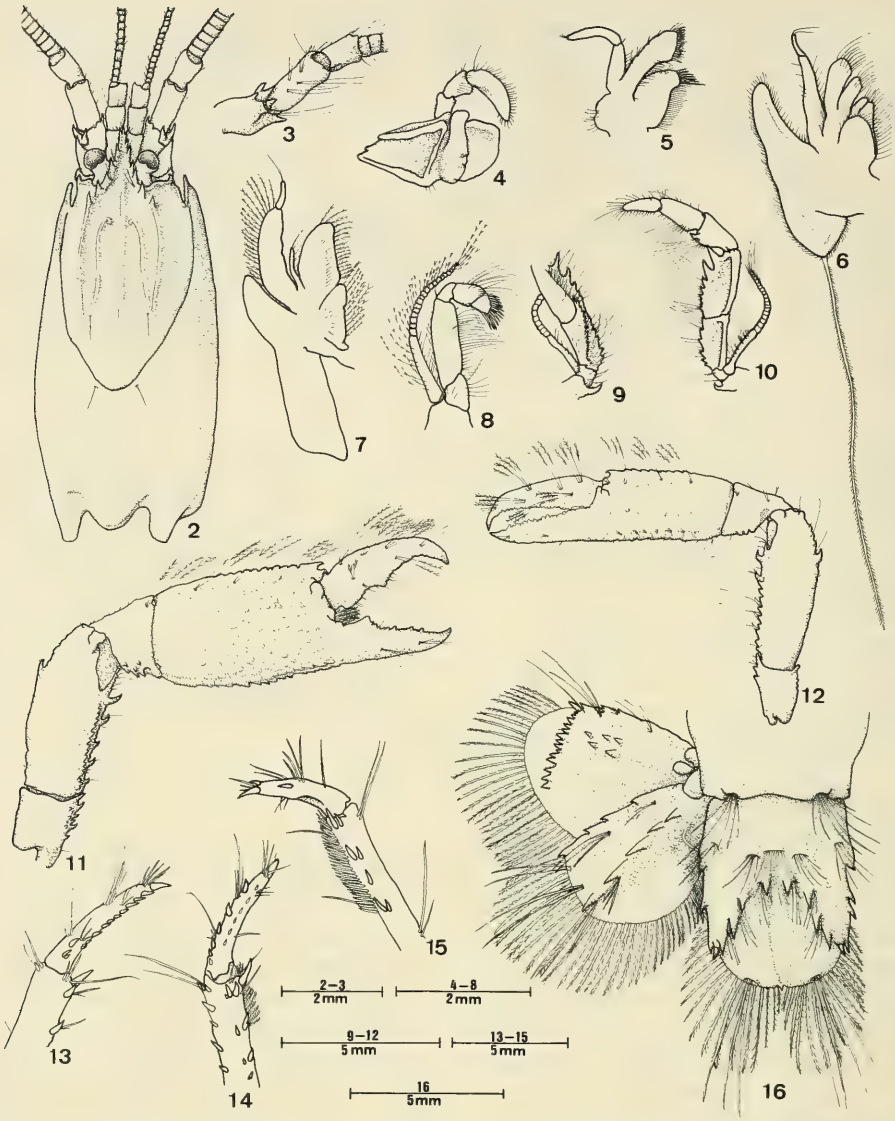


Fig. 1. *Eutrichocheles pindatyba,* new species, holotype in lateral view.

low teeth. Smaller chela (Fig. 12), ischium, merus, and carpus as in larger chela, fingers almost as long as propodal palm, latter with margins as in larger chela but surfaces less tuberculate, fingers with cutting edges nearly straight, denticulate. Pereopod 2, merus of right leg with tooth on posterior margin distal to midlength; pereopods 3–5 (Figs. 13–15) each with several strong spines on propodus and dactylus. Pleopods lacking appendix interna. Uropod (Fig. 16), outer ramus with 3 distal teeth on lateral margin, mobile spine at articulation of suture, 14 teeth along suture, 5 dorsal teeth on lateral ridge; inner ramus with 4 teeth on lateral margin, 5 teeth along dorsal ridge. Telson (Fig. 16), lateral margins with 3 teeth on left side, 4 on right, anterior to moderately long mobile spine; posterior margin convex with median tooth, 4 pairs of strong teeth on dorsal surface.

Etymology.—The specific epithet is derived from the Tupi Amerindian language: 'pinda' for hook or spine, and 'tyba' for 'many,' and refers to the numerous spines on the rostrum and appendages.

Remarks.—*Eutrichocheles pindatyba* is at once distinguished from the other species attributed to the genus by the more numerous teeth of the rostrum. It also differs from *E. modestus* (Herbst, 1796), and *E. defensus* (Rathbun, 1901) by the absence of teeth or tubercles along the carinae of the gastric region. In *E. bisquamosus* (de Man, 1905) the gastric region is unusual in lacking submedian and lateral carinae. The features of the gastric region of *E. johnstoni* (Edmondson, 1925) were not described, but other differences, such as the absence of teeth on the ischium of pereopod 1 and the lower number of teeth on the dorsal carina of the inner uropodal ramus, can be noted from Edmondson's figure 4. De Man (1925) in his key to the species of the subgenus *Parax-*



Figs. 2–16. *Eutrichocheles pindatyba,* new species, holotype: 2, carapace in dorsal view; 3, antennal peduncle; 4, mandible; 5, maxilla 1; 6, maxilla 2; 7, maxilliped 1; 8, maxilliped 2; 9, maxilliped 3, inner surface of merus and ischium; 10, maxilliped 3, outer surface; 11, pereopod 1, larger cheliped; 12, pereopod 1, smaller cheliped; 13, pereopod 3, distal propodus and dactylus; 14, pereopod 4, distal propodus and dactylus; 15, pereopod 5, distal propodus and dactylus; 16, telson and left uropod in dorsal view.

iopsis includes *A.* (*P.*) *aethiopica* Nobili, 1904, which Sakai & de Saint Laurent (1989) include in their new genus *Allaxius.* The more numerous teeth on the gastric region of the carapace and the smaller teeth of the ischium and merus of pereopod 1 in the Red Sea species separate it from the new Brazilian species.

The few other records of axiids from Brazil include *Axiopsis serratifrons* (A. Milne Edwards, 1873), known from Bahia and Paraiba, (S. Rodrigues, personal records),

Table 1.—Distribution of gills, epipods, and exopods in *Eutrichocheles pindatyba.*

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	—	—	—	—	—	—	—	—
Arthrobranchs	—	—	2	2	2	2	2	—
Podobranchs	—	—	—	—	—	—	—	—
Epipods	1	1	1	1	1	1	1	—
Exopods	1	1	1	—	—	—	—	—

the probably erroneous identification of the Californian species *Axiopsis spinulicauda* (Rathbun, 1902) from Amapá, (see Coelho et al. 1980:58, 59, 125), and *Axiopsis* sp. from tropical Brazil (see Coelho 1969:231). *Calastacus angulatus* and *Calastacus spinosus,* both described by Coelho (1973) from northern Brazil, if true *Calastacus,* are members of the Calocarididae, not the Axiidae.

Acknowledgments

We are grateful to Dr. Martin L. Christoffersen for the loan of the specimen described here; to Mr. Roberto M. Shimizu for the illustrations; to the Smithsonian Institution for a short-term fellowship to one of us (SAR). We thank Drs. Raymond B. Manning and Austin B. Williams for their useful comments on reading this paper.

Literature Cited

Balss, H. 1933. Ueber einige systematisch interessante indopacifische Dekapoden.—Mitteilungen aus dem Zoologischen Museum in Berlin 19:84–97.

Chopra, B. 1933. Further notes on Crustacea Decapoda in the Indian Museum V. On *Eutrichocheles modestus* (Herbst): Family Axiidae.—Records of the Indian Museum 35(3):277–281.

Coelho, P. A. 1969. A distribuiçao dos crustáceos decápodos reptantes do norte do Brasil.—Trabalhos Oceanograficos, Universidade Federal de Pernambuco, Recife 9/11:223–238.

———. 1973. Descriçao preliminar de *Calastacus angulatus,* n. sp. e de *C. spinosus* n. sp., do Norte do Brasil (Crustacea, Decapoda, Axiidae).—Ciencia e Cultura, supplemento 25(6):344–345.

———, M. Ramos Porto, & M. L. Koening. 1980. Biogeografia e bionomia dos crustáceos do litoral equatorial Brasileiro.—Trabalhos Oceanográficos, Universidade Federal de Pernambuco, Recife 15:7–138.

Edmondson, C. H. 1925. Marine Zoology of Tropical Central Pacific. Crustacea.—Bulletin of the Bernice P. Bishop Museum 27:3–62.

Herbst, J. F. W. 1796. Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten, vol. 2, (1791-1796):i-viii, 1–226.

Holthuis, L. B. 1986. J. C. Fabricius' (1798) species of *Astacus,* with an account of *Homarus capensis* (Herbst) and *Eutrichocheles modestus* (Herbst) (Decapoda Macrura).—Crustaceana 50(3):243–256.

Man, J. G. de. 1905. Diagnoses of new species of macrurous decapod Crustacea from the "Siboga-Expedition."—Tijdschrift der Nederlandsche Dierkundige Vereeniging (2)9(3/4):587–614.

———. 1925. The Decapoda of the Siboga-Expedition. Part 6. The Axiidae collected by the Siboga-Expedition.—Siboga Expeditie 39a(5):1–128.

Milne Edwards, A. 1873. Description de quelques Crustacés nouveaux ou peu connus provenant du Musée de M. C. Godeffroy.—Journal de Museum Godeffroy 4:77–88.

Nobili, G. 1904. Diagnoses préliminaires de vingt-huit espèces nouvelles de stomatopodes et decapodes Macroures de la Mer Rouge.—Bulletin du Muséum National d'Histoire Naturelle, Paris 10:228–237.

Rathbun, M. J. 1901. The Brachyura and Macrura of Porto Rico.—U.S. Fish Commission Bulletin for 1900, 2:1–137.

———. 1902. Descriptions of new decapod crustaceans from the west coast of North America.—Proceedings of the United States National Museum 24(1272):885–905.

Sakai, K., & M. de Saint Laurent. 1989. A check list of Axiidae (Decapoda, Crustacea, Thalassinidea, Anomura), with remarks and in addition descriptions of one new family, eleven new gen-

era and two new species.—Naturalists [Tokushima Biological Laboratory, Shikoku Women's University, Japan] 3:1–104.

Wood Mason, J. 1876. On new or little-known crustaceans.—Proceedings of the Asiatic Society of Bengal for 1875:230–232.

(SAR) Departamento de Ecologia Geral, Instituto de Biociéncias, Universidade de São Paulo, C. Postal 11461, 05499 São Paulo, Brazil; (BK) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 561–568

A LARGE BRACHYURAN-LIKE LARVA OF THE HIPPIDAE (CRUSTACEA: DECAPODA: ANOMURA) FROM THE BANDA SEA, INDONESIA: THE LARGEST KNOWN ZOEA

Joel W. Martin and Bernard Ormsby

Abstract.—A collection of planktonic Crustacea from the Banda Sea, Indonesia, contained several specimens of a large, late stage zoea belonging to the anomuran family Hippidae. As is true for the few previous descriptions of hippid larvae, the zoea bears a remarkable (but superficial) similarity to larvae of true crabs (Brachyura) in that the carapace is spherical and the lateral and rostral spines are distinctly deflected ventrally. The zoea is also remarkable in its size; the width across the lateral carapace spines is over 12.0 mm, making this the largest known zoea of the Anomura or Brachyura. Characters of the zoea are compared to previous descriptions of hippid larvae.

Planktonic larval stages of the decapod crustacean infraorders Brachyura and Anomura are usually easy to distinguish. The two most obvious characters concern the carapace: in anomurans the carapace is longer than broad, and the rostral spine is directed anteriorly, whereas in brachyuran larvae the carapace is spherical and the rostral spine (usually present) is directed ventrally (see Williamson 1982). Another differentiating character is that the sixth abdominal segment, in later stages, always bears setose uropods in the Anomura, whereas uropods are absent in zoeal stages of the Brachyura (except for raninids, homolids, and some other "primitive" crab families; Rice 1980, Martin 1991). Also, most anomuran larvae have a hair-like process between the first and third posterior spines on the telson, although this condition changes with ontogeny (Konishi 1989, Martin 1991).

The present paper describes a large zoeal stage of the anomuran superfamily Hippoidea. The zoea is of interest not only for its great size (over 6.0 mm carapace length, and over 12.0 mm in carapace width, including the lateral carapace spines), making it the largest known zoea in the Decapoda, but because, like previously described larvae of the Hippoidea, it is superficially similar to zoeal stages of the Brachyura.

Materials and Methods

Zooplankton samples were collected during an expedition of the R/V *Alpha Helix* to the area of the Banda Sea, Indonesia, in 1975. One lot contained 7 large, late stage zoeae that we herein assign to the anomuran family Hippidae; this lot was collected in the south Ceram Sea, just northwest of the island of Ceram (sometimes spelled Seram), at AH Station 19 (3°55.7′S, 128°07.7′E, trawl RMT-8, 0–150 m). An additional lot containing 4 specimens of this same zoeal stage was later found in collections from AH Station 28, also in the Ceram Sea (3°14.8′S, 127°38.0′E, trawl RMT-8, 0–100 m). Zooplankton was collected with an otter trawl fitted with a 0.5 mm mesh plankton net. Most of the crustacean samples from this expedition, including those with the hippid zoeae, dried out completely before they came to our attention (early 1989). Some of the larvae were rehydrated in Trisodium Phos-

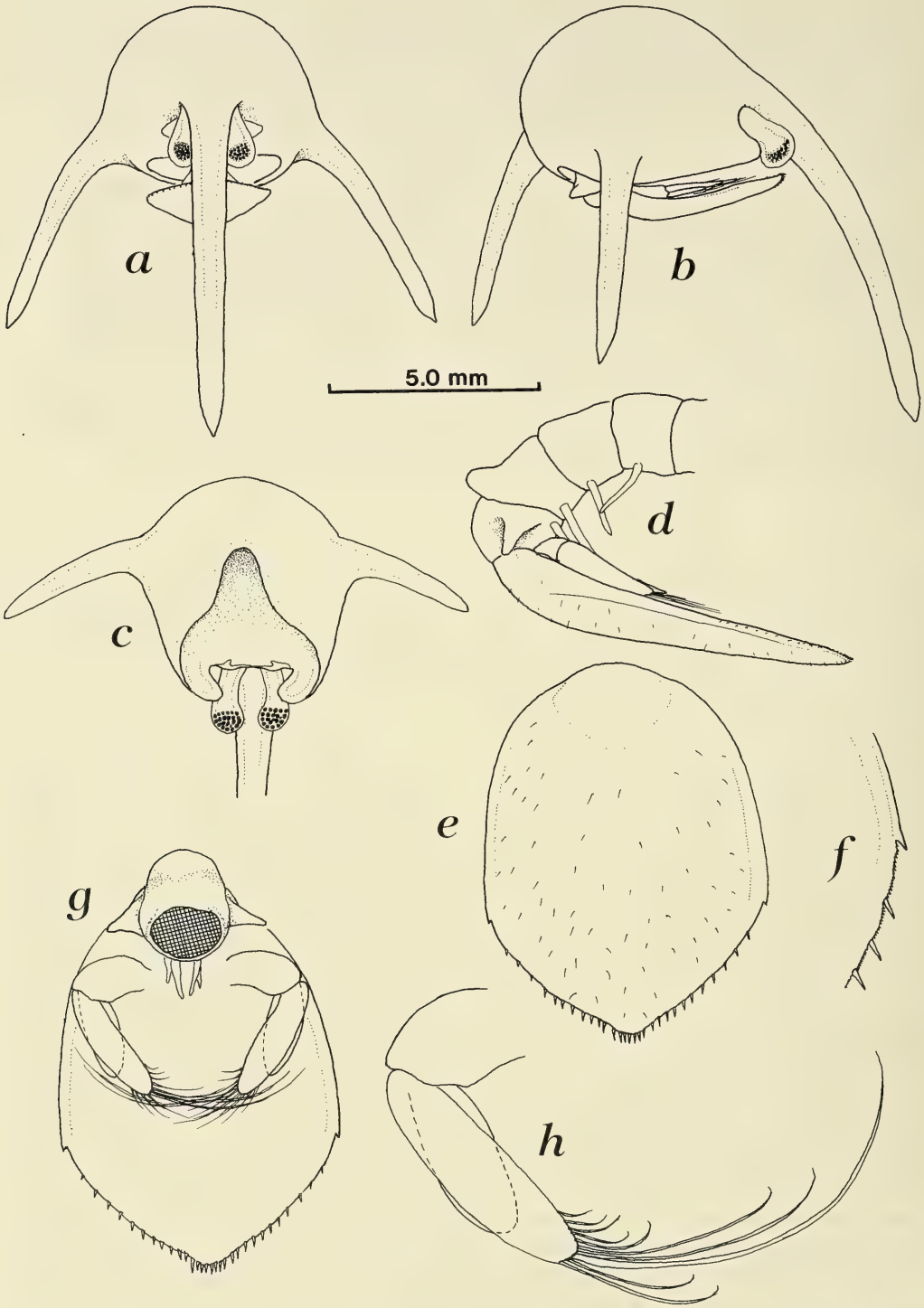


Fig. 1. Large hippid zoea from the Banda Sea, Indonesia: carapace, abdomen, and telson. a, entire zoea, frontal view; b, same, side view; c, ventral view of carapace and spines with telson and abdomen removed (note how ventral carapace is shaped to conform to opercular-like telson; d, lateral view of abdomen and telson; e,

phate for a period of 48 hours and then transferred to 70% ethanol. A few of the larvae were left dry. All drawings were made with a Wild M5APO dissecting microscope and a Zeiss compound stereoscope, each with camera lucida, from specimens collected at AH Station 19. Measurements were made from the single largest zoea, which was among the four specimens taken at AH Station 28.

Description

Size.—Carapace length 6.5 mm (from orbit to posterior border of carapace, allowing for slight curvature); carapace width (excluding lateral spines) 6.3 mm; length of rostral spine 10.8 mm; length of lateral spine 6.8 mm; distance from tip to tip of lateral spines 12.3 mm.

Stage.—Because of the large size and the development of the pleopods and uropods, this is probably a late stage zoea, equivalent to a stage 4 or later larva as compared to earlier accounts of development in the Hippidae (e.g., Hanson 1969).

Carapace (Fig. 1a, b, c).—Cephalothorax smooth, weakly calcified, globose, with extremely long downcurved rostral spine (longer than carapace length) and slightly downcurved lateral spines (less than rostral length). No dorsal spine noted in this stage.

Abdomen (Fig. 1d, g).—Five articulating somites, with the sixth fused to the telson. Somites 2 through 5 with pleopods. Somite length and width roughly equal. Fifth somite with blunt ventrolateral protrusions extending slightly posteriorly. Abdomen tightly flexed forward, with telson expanded and covering pereiopods and mouthparts ventrally.

Telson (Fig. 1e, f, g).—Longer than broad, terminally subtriangular. Dorsal surface with scattered short setae. Posterior border with sharp spines separated by minute serrations; spines becoming more dense approaching posterior terminus of telson. One immovable tooth (Fig. 1f) on either side of lateral border at about two thirds length of telson.

Uropods (Fig. 1g, h).—Long, extending approximately half length of telson (more than half if extended fully or if setation considered), biramous, outer ramus bearing 8–10 long simple setae, inner ramus unarmed.

First antenna (*antennule*) (Fig. 2a).—Stout, distal portion with 5 tiers containing aesthetascs.

Second antenna (Fig. 2b).—Protopod with three paired, evenly spaced spines, becoming progressively shorter distally; terminus of protopod spine-like; single spine located at articulation of endopod. Endopod extending nearly to tip of protopod, with three spines, tapering to acute distal tip; total length of endopod approximately ⅛ length of protopod.

Mandible (Fig. 2c).—Anterior border with 1 sharp and 1 blunt tooth, both of which exceed length of denticle row. Denticles acute, sclerotized, subequal in length, numbering 7–8.

Maxillule (Fig. 2d).—Endopod consisting of a single segment with 1 long, minutely serrulate, terminal seta. Exopod bilobed; basal endite with 3 stout serrate spines on distal margin; coxal endite with 1 short proximal seta, and 4 longer minutely serrulate setae distally, 3 of which are in distal group.

Maxilla (Fig. 2e).—Endopod with two simple and two plumose setae on margin plus one long simple seta on distal terminus. Endite not seen. Scaphognathite with numerous plumose setae spaced as illustrated.

Maxilliped 1 (Fig. 2f).—Basis bearing 5–7 plumose setae usually arranged in pairs;

←

dorsal (functional ventral) surface of telson showing indistinct fusion of telson with 6th abdominal somite (light stippling); f, higher magnification of lateral tooth and spines on right side of figure e; g, ventral surface of telson with uropods and abdominal somites 5 and 6 in place (stippled area denotes removed abdominal somite); h, right uropod. Scale bar corresponds to figures a–c only.

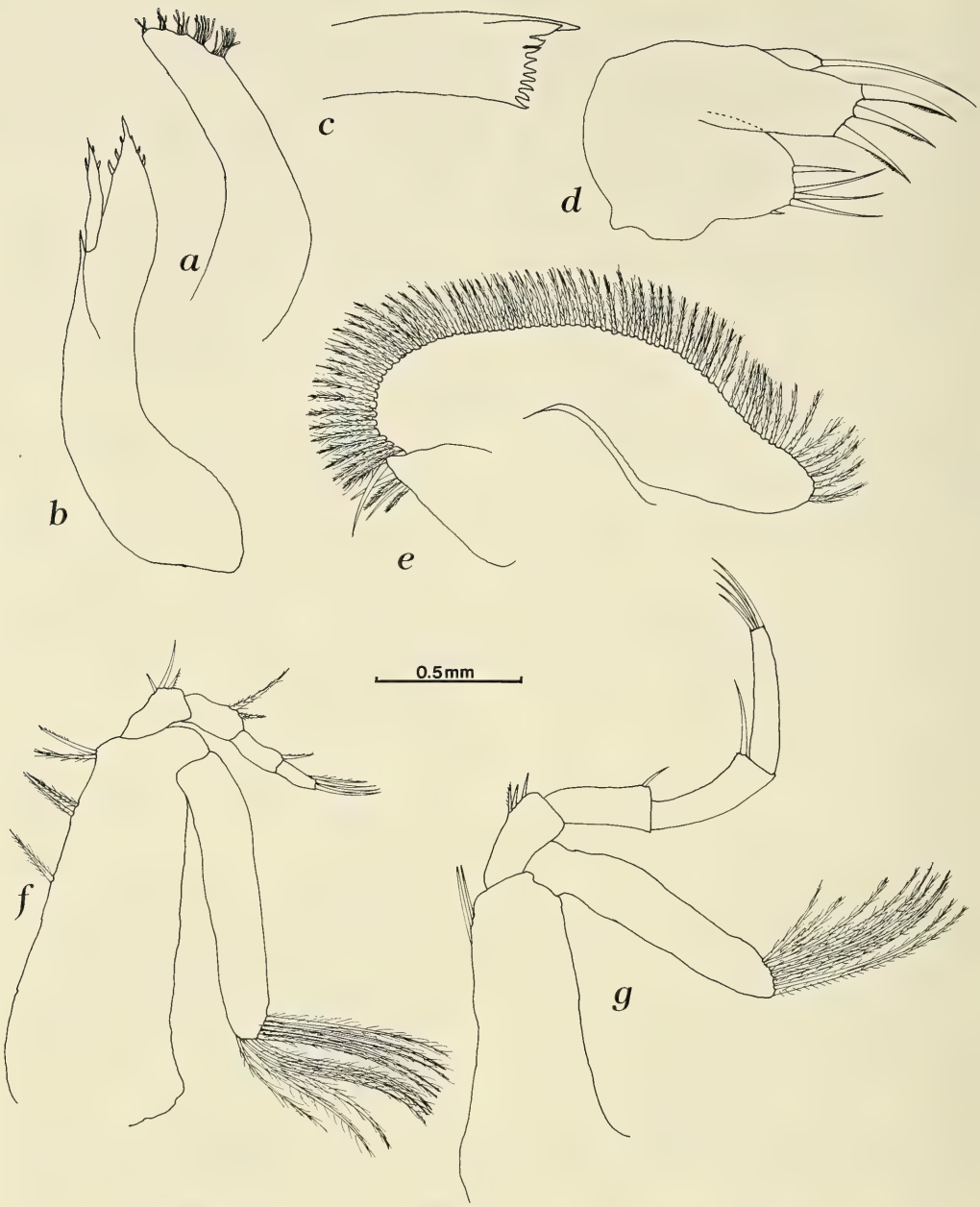


Fig. 2. Large hippid zoea from the Banda Sea, Indonesia: antennae and mouthparts. a, first antenna; b, second antenna; c, inner view of left mandible; d, maxillule; e, maxilla; f, first maxilliped; g, second maxilliped. Scale bar applies to all figures.

endopod 4-segmented, with setation 3, 2, 1, 4 (proximal to distal). Exopod uniramous with 10–12 natatory setae distally.

Maxilliped 2 (Fig. 2g).—Basis with two plumose setae; endopod 4-segmented, setation 3, 1, 1, 4 (proximal to distal); exopod with 9 to 11 natatory setae.

Maxilliped 3.—Present only as small undeveloped bud.

Pleopods (Fig. 1d).—Well developed, ex-

tending from somites 2 through 5, uniramous.

Discussion

The Banda Sea zoea is probably a late stage larva. The large size, coupled with the well developed pleopods and uropods, indicate to us that this zoea is at least in stage 4 or higher, if development proceeds as in other genera of the Hippoidea (e.g., Hanson 1969).

Of the two families, Albuneidae and Hippidae, that comprise the anomuran superfamily Hippoidea, larvae are best known for the albuneids, with larval stages of at least four genera known (e.g., Johnson & Lewis 1942, Knight 1970, Sandifer & Van Engel 1972, Gore & Van Dover 1980, and Stuck & Truesdale 1986, for *Lepidopa*; Menon 1937, and Seridji 1988, for *Albunea*; Johnson & Lewis 1942, Boschi et al. 1968, and Knight 1968, for *Blepharipoda*; Konishi 1987, for *Lophomastix*). Seridji (1988:1299) presented a table comparing larval characteristics of the "three known genera of the Albuneidae." However, Seridji apparently was unaware of the genus *Lophomastix,* for which larvae of one species have been described (Konishi 1987), and the genera *Leucolepidopa, Paralbunea, Zygopa, Austrolepidopa,* and *Stemonopa* (see Efford & Haig 1968, Efford 1969, Haig 1974b, Serène 1979), for which no larvae have been described. The major distinguishing character separating hippid larvae and albuneid larvae, according to Seridji (1988), is that albuneids have uniramous pleopods in later zoeal stages. This distinction does not always hold true, as Stuck & Truesdale (1986) documented biramous pleopods (albeit minutely biramous) in a fourth stage zoea of an albuneid (*Lepidopa benedicti*). No known albuneid larva has uropods as distinctly biramous as in the zoea described herein. Additionally, all known albuneid larvae possess a distinctive rhomboid-shaped telson that is always wider than long and is posteriorly somewhat truncate. The first and third, or first and fourth, teeth on the posterior border of the telson are strong and well developed. In contrast, the telsons in hippid larvae tend to be terminally rounded, with only the first posterior process modified as a strong immovable tooth, like the telson of the larva described here. Our larvae clearly belong to the Hippidae rather than to the Albuneidae.

Assignment to Genus

Assignment to a particular hippid genus is more difficult. There are currently three accepted genera in the Hippidae: *Emerita* Scopoli, *Hippa* Fabricius, and *Mastigochirus* Miers (see Haig 1970). Larvae are known only for *Hippa* and *Emerita,* and the zoeal stages of species in these two genera are extremely similar. Hanson (1969), in the only description of a complete larval series of a species of *Hippa* (*H. cubensis* (De Saussure)), mentioned that larvae of the two genera differ only in that zoeae of *Emerita* bear fewer aesthetascs on the antennule, fewer spines on the telson, fewer setae on the scaphognathite border, and are generally smaller than zoeae of *Hippa.* Hanson's (1969) description was actually of larvae of *H. testudinaria* (Herbst), rather than *H. cubensis,* according to Haig (1970). Hanson's comparison with species of *Emerita* was based on the work of Menon (1933), Johnson & Lewis (1942), Rees (1959), and Knight (1967). The descriptions of Smith (1877) and Faxon (1879) of larvae of *Hippa* were actually of species in *Emerita.* Hanson (1969) also mentioned that "The antenna of *Emerita* develops a long flagellum in the fourth or fifth zoeal stage" that persists through the megalopa stage, whereas this flagellum "is entirely lacking in *Hippa*" (Hanson 1969:155), and he related the above morphological differences to differences in feeding modes between the two genera, species of *Hippa* being scavengers rather than filter feeders. Our zoea is closer to Hanson's description of larvae of *H. testudinaria* than to existing descriptions of *Emerita* larvae

(e.g., Knight 1967 for *E. rathbunae*). Consequently, we tentatively assign our large zoea to *Hippa.*

An additional character strengthening the assignment of the Band Sea larvae to *Hippa* is that in Hanson's description of *H. testudinaria* larvae there is a noticeable ventrolateral projection extending from the posterior border of the fifth abdominal somite, similar to the condition of the Banda Sea zoea. This is also seen in plankton-collected stages attributed to *Hippa* by Lebour (1959: fig. 17) and to a lesser extent in the figures of Al-Kholy (1959: figs. 40–48). We have not seen this character in descriptions of *Emerita* larvae. Our zoea differs from Hanson's (1969) description of the larvae of *H. testudinaria* mostly in size. Hanson's largest zoea, at stage VI, had a carapace length of only 3.87 mm, whereas the Banda Sea zoea has a CL of 6.5 mm, which is even larger than the megalopa stage of *H. testudinaria.* The two species also differ morphologically; the Banda Sea zoea has a more strongly curved rostral spine, paired spines on the second antenna, and a single (unpaired) ventral tooth on the distal mandible border (compare to Hanson's fig. 3a).

Because of the above-mentioned uncertainty concerning generic placement of our larvae, the geographic distribution of all hippid genera should be considered in trying to assign the Banda Sea larvae. The geographically closest species of *Emerita* would be *E. emeritus* (Linnaeus), which, according to Efford (1976), ranges from the west coast of India east to southern Sumatra. At least one species of *Mastigochirus, M. quadrilobatus* Miers, is known from western Australia and Queensland and westward into the central sector of the Indian Ocean (Haig 1974a, 1974b); the only other known species in the genus, *M. gracilis* (Stimpson), also inhabits the Indo-West Pacific (China Sea and Sri Lanka, Haig 1974a). *Hippa* is the largest of the three hippid genera and is represented in the tropical western Pacific by at least 10 species, three of which, *H. adactyla, H. pacifica,* and *H. celaeno,* are widely distributed in the Indian and Indo-West Pacific Oceans (Haig 1974a). Therefore, known geographic distributions of species in the three hippid genera would also suggest the probability that the zoea described herein belongs to *Hippa.*

We confirm, if our larvae and those of *H. testudinaria* are typical for the genus *Hippa,* and if our zoea does in fact belong to a species of *Hippa* rather than to *Mastigochirus,* that larval size is quite different between the genera *Hippa* and *Emerita.* Our zoea, with a carapace length of over 6.0 mm (excluding the rostral spine) and with a distance of over 12.0 mm between the tips of the lateral spines, exceeds that for any known larval stage, including the megalopal stages, of any species of *Emerita.* Indeed, this zoea is larger than any zoea, and even megalopa, of the Brachyura reported in the survey of Hines (1986). To the best of our knowledge, the zoea described in this paper, while smaller than some of the unusual larvae of palinurid and eryonoid lobsters, which have phyllosoma and eryoneichus larvae sometimes considered "zoeal" (e.g., Williamson 1969), is the largest known zoeal stage among the decapod Crustacea.

Acknowledgments

We are very grateful to Janet Haig, Frank Truesdale, and Pedro Báez R. for review of the manuscript and for assistance with the literature. We thank Hans G. Kuck for recognizing the unusual size of the specimens and bringing them to our attention, and Ms. Jennifer Christiansen for assisting with sorting and preliminary identification of the plankton. Special thanks are extended to the Ichthyology Section of the Natural History Museum of Los Angeles County for donating the specimens.

Literature Cited

Al-Kholy, A. A. 1959. Larval stages of three anomuran Crustacea.—Publications of the Marine

Biological Station, Al-Ghardaqa, Egypt 10:83–89, pls. 1–4.

Boschi, E. E., B. Goldstein, & M. A. Scelzo. 1968. Metamorfosis del crustáceo *Blepharipoda doelloi* Schmitt de las aguas de la Provincia de Buenos Aires (Decapoda, Anomura, Albuneidae).—Physis (Buenos Aires) 27:291–311.

Efford, I. E. 1969. *Leucolepidopa sunda,* gen. nov., sp. nov. (Decapoda: Albuneidae), a new Indo-Pacific sand crab.—Breviora 318:1–9.

———. 1976. Distribution of the sand crabs in the genus *Emerita* (Decapoda, Hippidae).—Crustaceana 30:169–183.

———, & J. Haig. 1968. Two new genera and three new species of crabs (Decapoda: Anomura: Albuneidae) from Australia.—Australian Journal of Zoology 16:897–914.

Faxon, W. 1879. On some young stages in the development of *Hippa, Porcellana,* and *Pinnixa.*—Bulletin of the Museum of Comparative Zoology, Harvard University 5:303–330.

Gore, R. H., & C. L. Van Dover. 1980. Studies on decapod Crustacea from the Indian River region of Florida. XIX. Larval development in the laboratory of *Lepidopa richmondi* Benedict, 1903, with notes on larvae of American species in the genus (Anomura: Albuneidae).—Proceedings of the Biological Society of Washington 93:1016–1034.

Haig, J. 1970. The status of *Remipes testudinarius* Latrielle, and designation of a neotype for *Hippa adactyla* J. C. Fabricius (Decapoda, Hippidae).—Crustaceana 19:288–296.

———. 1974a. A review of the Australian crabs of family Hippidae (Crustacea, Decapoda, Anomura).—Museum of Queensland Memoir 17: 175–189.

———. 1974b. The anomuran crabs of western Australia: their distribution in the Indian Ocean and adjacent seas.—Journal of the Marine Biological Association of India 14:443–451.

Hanson, A. J. 1969. The larval development of the sand crab *Hippa cubensis* (De Saussure) in the laboratory (Decapoda, Anomura).—Crustaceana 16:144–157.

Hines, A. H. 1986. Larval patterns in the life histories of brachyuran crabs (Crustacea, Decapoda, Brachyura).—Bulletin of Marine Science 39:444–466.

Johnson, M. W., & W. M. Lewis. 1942. Pelagic larval stages of the sand crabs *Emerita analoga* (Stimpson), *Blepharipoda occidentalis* Randall, and *Lepidopa myops* Stimpson.—Biological Bulletin 83:67–87.

Knight, M. D. 1967. The larval development of the sand crab *Emerita rathbunae* Schmitt (Decapoda, Hippidae).—Pacific Science 21:58–76.

———. 1968. The larval development of *Blepharipoda occidentalis* Randall and *B. spinimanus* (Philippi) (Decapoda, Albuneidae).—Proceedings of the California Academy of Sciences 35: 337–370.

———. 1970. The larval development of *Lepidopa myops* Stimpson (Decapoda, Albuneidae) reared in the laboratory, and the zoeal stages of another species of the genus from California and the Pacific coast of Baja California, Mexico.—Crustaceana 19:125–156.

Konishi, K. 1987. Larval development of the spiny sand crab *Lophomastix japonica* (Duruflé, 1889) (Crustacea, Anomura, Albuneidae) under laboratory conditions.—Publications of the Seto Marine Biological Laboratory 32(1/3):123–139.

———. 1989. Larval development of the mud shrimp *Upogebia* (*Upogebia*) *major* (De Haan) (Crustacea: Thalassinidea: Upogebiidae) under laboratory conditions, with comments on larval characters of thalassinid families.—Bulletin of the National Research Institute for Aquaculture 15:1–17.

Lebour, M. V. 1959. The larval decapod Crustacea of tropical West Africa.—Atlantide Reports 5: 119–143.

Martin, J. W. 1991. Crabs of the family Homolodromiidae, III. First record of the larvae.—Journal of Crustacean Biology 11:156–161.

Menon, M. K. 1933. The life-histories of decapod Crustacea from Madras. The life-histories of four species of decapod Crustacea from Madras.—Bulletin of the Madras Government Museum, New Series, Natural History 3:1–45.

———. 1937. Decapod larvae from the Madras plankton. I.—Bulletin of the Madras Government Museum, New Series, Natural History 3: 1–55.

Rees, G. H. 1959. Larval development of the sand crab *Emerita talpoida* (Say) in the laboratory.—Biological Bulletin 117:356–370.

Rice, A. L. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura.—Transactions of the Zoological Society of London 35:271–424.

Sandifer, P. A., & W. A. Van Engel. 1972. *Lepidopa* larvae (Crustacea, Decapoda, Albuneidae) from Virginia plankton.--Journal of the Elisha Mitchell Scientific Society 88:220–225.

Serène, R. 1979. Description of *Paralbunea manihinei* gen. and spec. nov. (Decapoda, Hippidae, Albuneidae).—Crustaceana, suppl. 5:95–99.

Seridji, R. 1988. Some planktonic larval stages of *Albunea carabus* (L., 1758) (Crustacea, Decapoda, Anomura).—Journal of Natural History 22: 1293–1300.

Smith, S. I. 1877. The early stages of *Hippa talpoida,*

with a note on the structure of the mandibles and maxillae in *Hippa* and *Remipes*.—Transactions of the Connecticut Academy of Science 3:311–324.

Stuck, K. C., & F. M. Truesdale. 1986. Larval and early postlarval development of *Lepidopa benedicti* Schmitt, 1935 (Anomura: Albuneidae) reared in the laboratory.—Journal of Crustacean Biology 6:89–110.

Williamson, D. I. 1969. Names of larvae in the Decapoda and Euphausiacea.—Crustaceana 16: 210–213.

Williamson, D. T. 1982. Larval morphology and diversity. Pp. 43–110 *in* L. G. Abele, ed., The biology of Crustacea, volume 2: embryology, morphology and genetics. Academic Press, New York, 440 pp.

Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 569–582

CRABS FROM THE MARIANA ARCHIPELAGO: *BOTHROMAIA GRIFFINI* NEW GENUS AND SPECIES (BRACHYURA: MAJIDAE), AND REMARKS ON *POUPINIA HIRSUTA* GUINOT (HOMOLOIDEA, POUPINIIDAE)

Austin B. Williams and Robert B. Moffitt

Abstract.—Deepwater trapping in the Mariana Archipelago, western North Pacific Ocean, included incidental catches of a spider crab and a homoloid crab with novel characteristics. *Bothromaia griffini,* new genus and species, family Majidae, subfamily Inachinae, represented by a male and female, seems most closely related to the genus *Pleistacantha* Miers, containing several species distributed in Indo-Pacific waters. The new species resembles members of this genus with respect to presence of pseudorostral horns, and shape of eyestalks, basal antennal article, epistome, third maxilliped, male sternites and pleopod 1, but differs from them in shape of pseudorostral horns, carapace, male pleopod, and in proportions of the ambulatory legs. Descriptions, illustrations, and comparative discussion are presented. Notes on the homoloid crab, *Poupinia hirsuta* Guinot, include locality data, measurements, remarks on distribution, and discussion of features distinguishing the families of Homoloidea, including a key for their identification.

During 1982–1984 field studies of the Resource Assessment Investigation of the Mariana Archipelago (RAIOMA) program in the western North Pacific Ocean, conducted by the National Marine Fisheries Service Southwest Fisheries Science Center Honolulu Laboratory, deepwater trapping operations concentrated on the pandalid shrimp species *Heterocarpus laevigatus* Bate, 1888 (see Polovina et al. 1985, Moffitt & Polovina 1987). Included in incidental trap catches was a female spider crab and a male homoloid crab with novel characteristics. Examination of additional preserved material from a 1971 trip to the same area yielded a male specimen of the spider crab that was collected in a shrimp trawl. The two spider crabs are herein described as a new genus and species of the family Majidae. The homoloid crab belongs to a species described from Raiatea, Society Islands, Polynesia, *Poupinia hirsuta* Guinot, 1991, that was placed in a new family Poupiniidae. Notes on the specimen reported here include locality data, measurements, discussion of structure and relationships, and a key to the homoloid families.

The specimens are deposited in the crustacean collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Comparative studies were made using collections of the USNM, the Australian Museum, Sydney (AMS), Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM), and the Queensland Museum, Brisbane, Australia (QM).

Family Majidae Samouelle, 1819
Subfamily Inachinae MacLeay, 1838
Bothromaia, new genus

Diagnosis.—Carapace pyriform, moderately broad, surface unevenly granular;

branchial regions swollen, deeply recessed urogastric region partly covered by projecting cardiac region and confluent anterolaterally with excavate cervical groove; conspicuous, slender spines on frontal, gastric, cardiac and branchial regions, and along anterolateral margins. Rostrum triangular, abruptly deflexed dorsally, ending in slender median spine; pseudorostral lobe near apex of antennular fossa distally ornamented with cluster of radiating spines. Supraorbital eave spinose, posterior margin of orbit open, allowing retraction of eyestalk. Eyestalks stout, small spine on corneal emargination. Basal antennular article broad, that of antenna long and not fused to front, both with ventral spines. Epistome broad. Merus of third maxilliped extended distally at distolateral corner, slightly narrower than ischium, merus and ischium spined ventrally. Cheliped of female (unknown in male) longer than carapace but only ⅔ length of first ambulatory leg. Ambulatory legs moderate in length, diminishing successively from first to last, somewhat flattened, setose, spiny, and granular on nearly all surfaces. First pleopod of male with shaft tapered, essentially straight except for distal section directed anterolaterally, subterminal aperture on mesial surface preceded by longitudinal tract of fine setae and succeeded by small spinelike process.

Type species.—*Bothromaia griffini* new species.

Etymology.—From the Greek, "bothros," trench, pit, hollow, and "maia," a kind of crab, with reference to the deep pit in the urogastric region. The gender is feminine.

Bothromaia griffini, new species
Figs. 1–4

Material.—Commonwealth of the Northern Mariana Islands: USNM 250884, holotype ♂, W of Saipan Island, 15°10.1′N, 145°39.9′E, 366–379 m, *Townsend Cromwell* cruise 53, sta 94, 30 Apr 1971, shrimp trawl (chelipeds missing, ambulatory legs separated from body).—250885, allotype ♀, Esmeralda Bank, 14°58.4′N, 145°15.8′E, 377 m, *Townsend Cromwell* cruise 82-02, sta 23 string 3, 23 Apr 1982, shrimp trap.

Measurements of carapace (mm).—Holotype ♂, overall length 33.3, fork length in midline 29, width to base of lateral spines 22, width including lateral spines (tips broken) 25.8; allotype ♀, same measurements 37.8, 36.7, 26.7, width including lateral spines 28.8.

Description.—Carapace pyriform, width about ⅔–¾ length, surface unevenly granular. Deeply recessed urogastric region confluent anterolaterally with excavate cervical groove.

Frontal region strongly depressed, triangular, ending in slender median (interantennular) spine directed anteriorly and slightly ventrad, tip slightly exceeding spine-tipped pseudorostral lobes at distolateral corner of each antennular fossa; pseudorostral lobes short (basal length 1.5 mm), blunt, bearing cluster of 4 radiating short spines apically; well developed spine below these near lateral margin of each antennular fossa flanked dorsally by smaller similar spine on lateral margin of pseudorostral lobe, and preceded by graduated series of spines on lateral margin of fossa, increasing to ventrolaterally projecting spine near its base.

Several spines on nearly semicircular supraorbital eave; margin bearing about 7 closely crowded small spines on anterior ⅓, much more scattered small spines on central and posterior ⅓; 3 much stronger submarginal spines (moderate anterior, very strong dorsal, smaller posterolateral); postorbital spine obscurely compound, but posterior margin of orbit open to allow retraction of eyestalk. Pair of strong epigastric spines posteromesial to pseudorostral lobes, pair of protogastric spines at anterior part of swollen gastric region; latter with 4 prominent spines at apices of rhombic array, anterior-most medial in middle of mesogastric region followed by 2 metagastrics projecting posterolaterally over right and left cervical

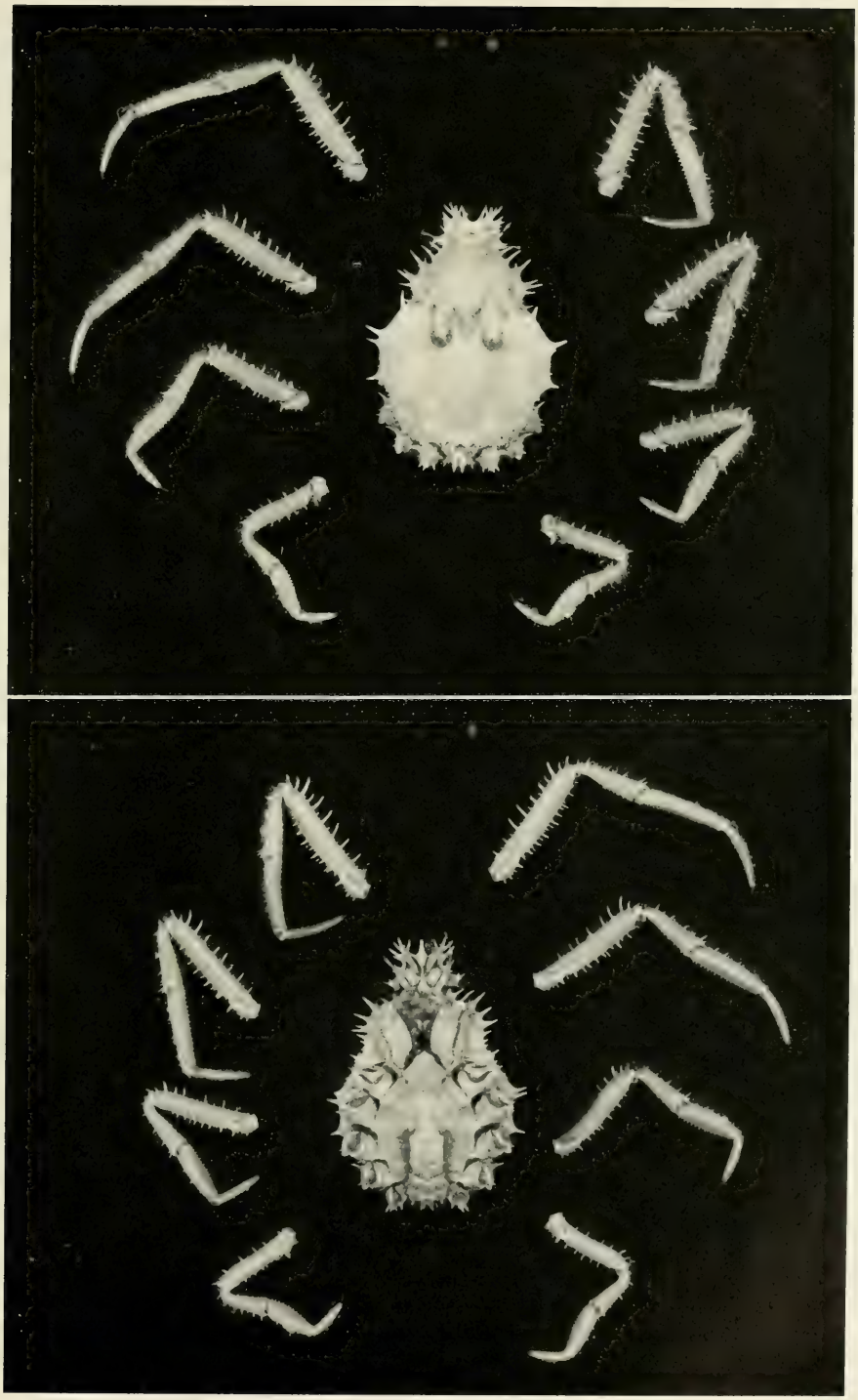


Fig. 1. *Bothromaia griffini,* new genus and species. Holotype ♂: upper, dorsal; lower, ventral (chelipeds missing, disarticulated legs arranged in order of succession).

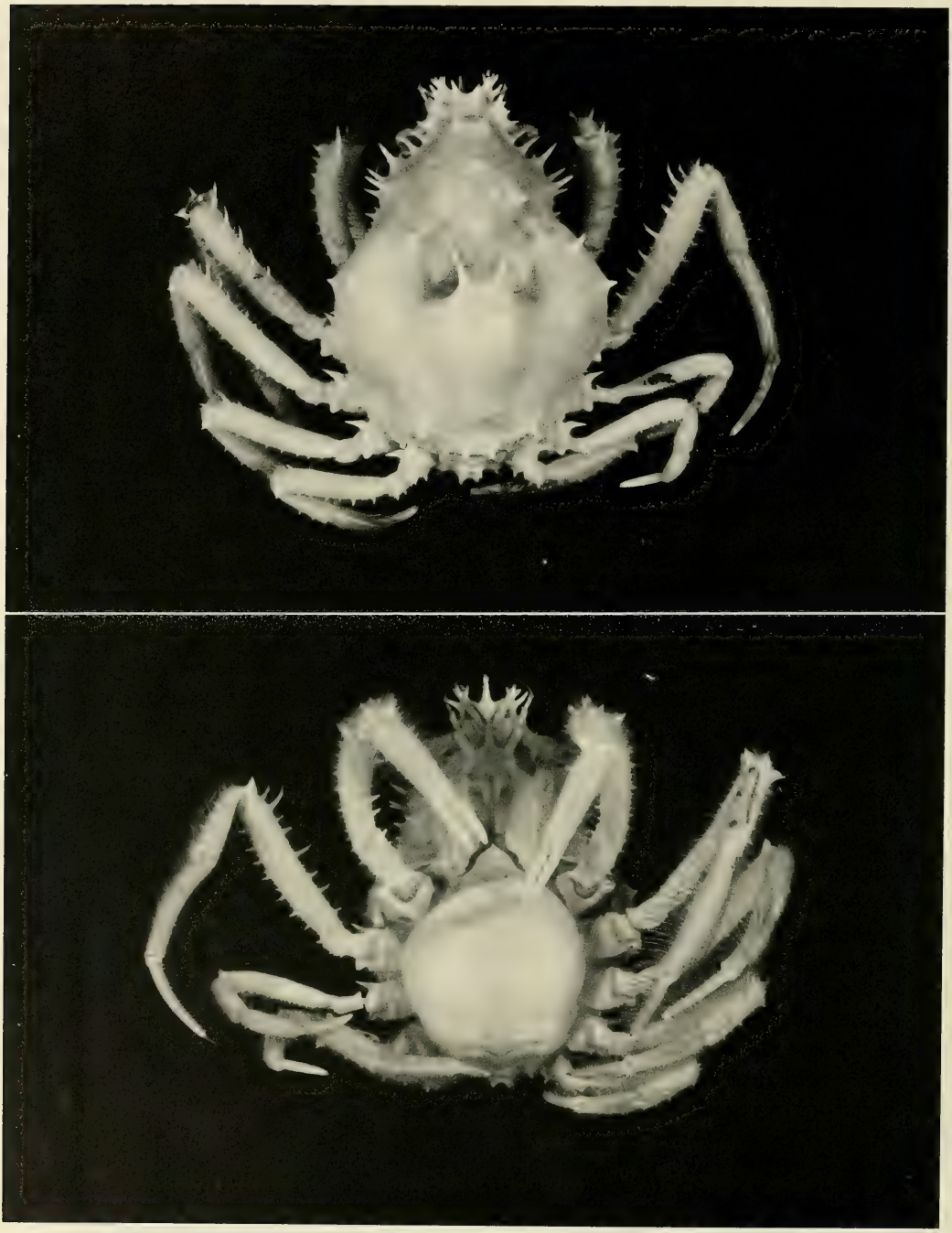


Fig. 2. *Bothromaia griffini,* new genus and species. Allotype ♀: upper, dorsal; lower, ventral.

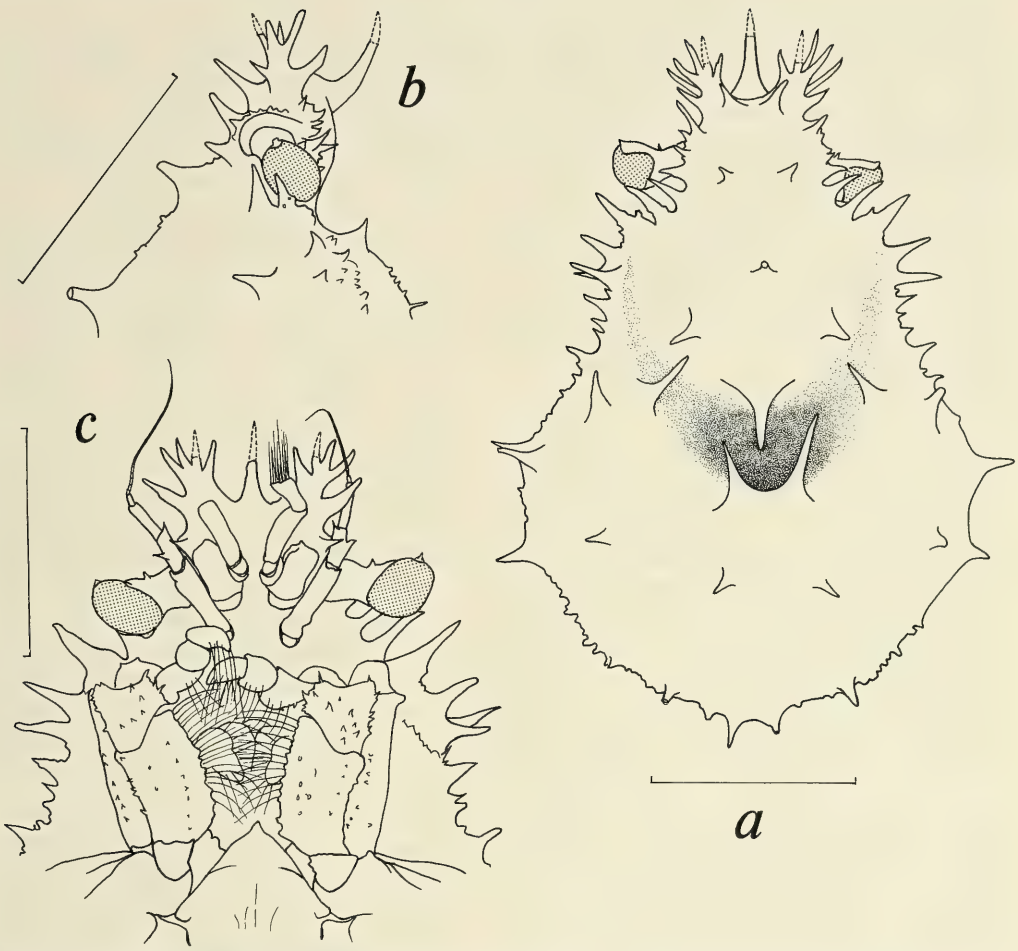


Fig. 3. *Bothromaia griffini,* new genus and species. Holotype ♂: a, carapace, dorsal; b, same, right lateral; c, cephalic region, ventral. Scales = 1 mm.

grooves, and posterior-most median extending posteriorly over recessed urogastric region. Cardiac region swollen and bearing 2 unequal pairs of spines; stronger anterior pair horizontally divergent from edge of regional extension over urogastric pit, shorter posterior pair near middle of region erect but laterally divergent. Intestinal region bearing pair of posteriorly projecting spines, stronger in male than in female. Each branchial region bearing 7 spines; large spine on anterior part of epibranchial region extending anteromesially over cervical groove, posterolateral to it another spine; mesobranchial region with dorsal spines at level of urogastric pit and cardiac region, and 2 others obliquely and lateroventrally in line with these respectively at perimeter of region; posterior-most spine near intestinal spines and well separated from preceding. Margin variably spiny in dorsal view, bearing 2 strong protogastric, 4 strong hepatic, and many smaller spines along branchial, posterolateral and intestinal sectors.

Eyestalks stout, bearing 2 small anterior spines on anterior surface of laterally extended eye, and 1 on corneal emargination, cornea twice width of stalk. Antennule with broad basal article spined ventrally. Basal antennal article slender, extending to basal

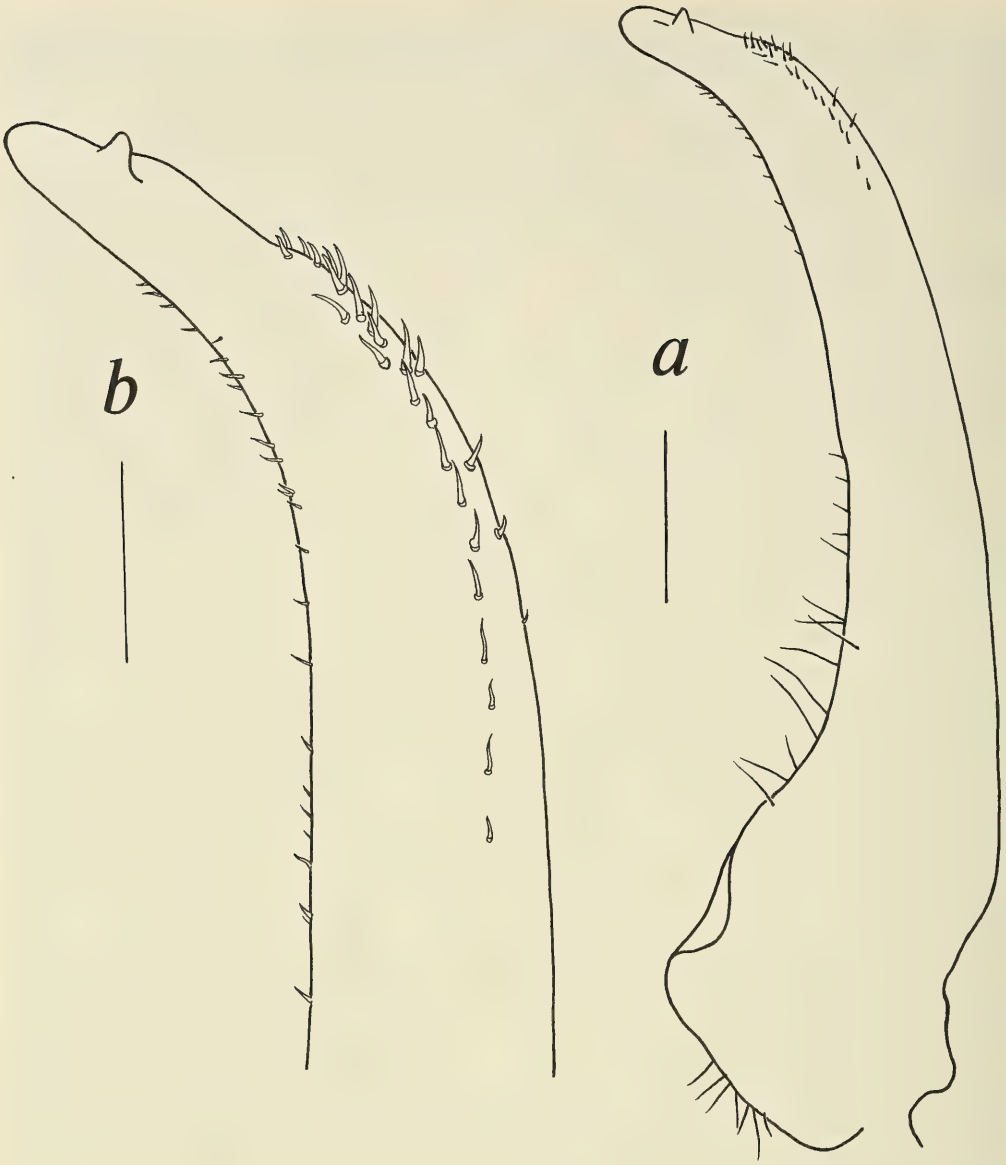


Fig. 4. *Bothromaia griffini* new genus and species. Holotype ♂ pleopod 1: a, abdominal view, b, magnified tip. Scales = 1 mm (a), 2.5 mm (b).

part of eyestalk, not fused to carapace, variably spined ventrally along mesial and lateral margins; middle and distal articles together reaching base of radiating spines on pseudorostral horn, middle article bearing ventral spine near middle of lateral margin and another spine variably developed at anteromesial corner.

Thoracic sternites of male bearing spines of varying sizes, most of them with seta originating near apex, and tendency to arrangement in submarginal row on each plate along radiating sutures; sternites of female not spinose, with raised thin lip where expanded 6th abdominal segment fits against them.

Abdomen of both sexes 6-segmented. That of female ampulliform in outline, with

narrow neck lodged between coxae of fifth legs, narrowest point at suture between segments 1 and 2 (5.6 mm), widest point at approximate midlength of broadly cupped, operculiform telson (17.7 mm); midlength of successive segments 1–6 (3.5, 3.0, 2.2, 2.3, 2.6, 14.9 mm); exposed surface of segments 2–6 sparsely but unevenly setose, densest on 2–4, becoming quite sparse on distal ⅓ of telson; segment 1 bearing submarginal median tubercle anteriorly, submedian pair of spines succeeding it, and scattered granules; segment 2 with 2 pairs of submedian setose granules and remote setose granule laterally, segments 3–5 with same pattern, but submedian granules successively more suppressed and lateral granule successively more remote from midline; margin of telson narrowly reflected distally, less definitely so laterally, broad subterminal depression near shallow terminal concavity (asymmetrical on allotype), definite marginal notch at coxal level of first ambulatory leg, faint tract of median ornamentation on anterior half reminiscent of that on preceding segments.

Abdomen of male not broadened but more or less parallel sided except for sinuosities of individual segments, ornamentation as in female except spines and granules magnified; segment 3 broadest (5.5 mm); telson subrectangular, as wide as long (4.1 mm), bearing posterolateral notch, narrowly reflected terminal margin concave and broadly sunken, pattern of ornamentation in proximal half resembling that on preceding segments. First pleopod reaching level of suture between sternites adjacent to coxae of first and second ambulatory legs; shaft tapered, essentially straight except for distal section curved anterolaterad, subterminal aperture on mesial surface preceded by longitudinal tract of fine setae and succeeded by short spinelike process.

Third maxilliped with ischium bearing ventral row of moderate spines along ventrolateral rib, few spines and setose granules scattered over remainder of exposed surface, mesial margin heavily setose and armed with few small stout spines more numerous in proximal than distal half of length; exognath armed with ventral row of rather strong spines and lateral row of much smaller spines. Merus slightly narrower than ischium, extended distally into subtriangular lobe at distolateral corner, margin irregularly spined, ventral surface with 2 curved rows of spines originating near articulation with ischium, each terminating in slender marginal spine at either side of articulation with carpus. Flexed carpus-propodus-dactyl reaching halfway along length of ischium.

Cheliped of female (missing on male specimen) densely setose except on fingers, slightly longer than carapace but only ⅔ length of first ambulatory leg; merus bearing 1 mesiodorsal row of strong spines, tract of shorter spines dorsolaterally tending to arrangement in 2 obscure rows, 2 rows of spines ventrally and row of irregular spines mesioventrally, stoutest spines on each merocarpal condyle and longest spines distally on dorsolateral row; carpus bearing scattered spines tending to arrangement in obscure rows; palm slender, somewhat flattened, bearing scattered small spines strongest on extensor surface; fingers just over ½ length of palm, nearly straight, leaving only small proximal gap when closed, uniformly crenulate on cutting edges of left hand (cutter), teeth slightly stronger in basal half of right dactyl (crusher), fingers of crusher worn or broken at tips, perhaps slightly spooned.

Ambulatory legs setose, spiny, and granular on nearly all surfaces, moderate length diminishing successively from first to last, somewhat flattened; coxae strongly spined anterolaterally, a few spines on ventromesial surface; ambulatory leg 1 about 1.5 times carapace length (basis to tip of dactyl in male ~51 mm), merus with 3 terminal spines, 2 of these lateral at apex of triangular merocarpal condyles, rows of spines on dorsal and ventral margins, dorsal row strongest, posterior surface bearing many scattered spinules, anterior surface less ornamented; carpus and propodus bearing single row of

small spines interspersed with longer spines on dorsal margin and scattered spines on posterior surface, crowded short spines and spiniform tubercles on ventral surface, many of them setose, anterior surface bearing few rows of setose granules; dactylus nearly as long as propodus and bearing many setae (sparse on anterior surface), but few small spines on prehensile surface, tip corneous. Succeeding ambulatory legs similar in ornamentation but successively shorter (length basis to tip of dactyl of male: leg 2, 50 mm; leg 3, 37 mm; leg 4, 33 mm).

Color.—A photograph of the allotype, taken against a light gray background at the time the specimen was collected, shows the overall color in dorsal view to be salmon; the frontal and gastric regions are darkest, but decorated by contrastingly lighter spines and tubercles of the same hue as the remainder of the body, including the legs; the cornea appears transparent.

Etymology.—The specific name honors D. J. G. Griffin, authority on majid crabs of the Pacific, and Director of the Australian Museum, Sydney.

Remarks.—*Bothromaia griffini* was studied with the aid of comparative reference to the discussions of *Pleistacantha* and *Cyrtomaia* species by Guinot (1985), Guinot & Richer de Forges (1982a, 1982b, 1985), Griffin & Tranter (1986), and Richer de Forges & Guinot (1988), and by comparisons with specimens in museum collections mentioned above. Depending on authority, *Pleistacantha* is regarded as containing 11 species and *Cyrtomaia* 24, all of which occur in deep waters of the Indo-Pacific.

Bothromaia seems closely allied to *Pleistacantha* Miers, 1879 in respect to: (1) shape of abruptly deflexed interantennular spine, although tip is bifurcate in some species of latter; (2) presence of armed pseudorostral horns; (3) well-developed eyestalks bearing expanded ovate cornea, with small spines on anterior surface of stalk and at corneal emargination; (4) basal antennal article slender, not fixed to front and bearing ventral spines; (5) epistome broad; (6) shape of ischium and merus of third maxilliped, (7) spined sternites on males; and (8) general conformation of male first pleopods.

Bothromaia differs from *Pleistacantha* in having: (1) short lobular pseudorostral horns, each bearing radiating cluster of spines at tip rather than being elongate horns armed with spines along length; (2) carapace rather inflated and relatively smooth on gastric and branchial regions bearing few conspicuous spines, and with deep urogastric pit confluent with excavated cervical groove overhung by extension of cardiac region as well as spines from it and neighboring regions, whereas that of *Pleistacantha,* somewhat depressed and lacking any evidence of urogastric pit, is densely armed with short spines; (3) ambulatory legs moderate in length, somewhat flattened, having rather stout meri, densely clothed with setae, spined, and fairly coarsely granulate, whereas those of *Pleistacantha* are long, cylindrical and spidery; (4) male first pleopods generally shaped as those in *Pleistacantha* species, but more obliquely angled terminal part, with aperture preceded by linear cluster of small setae, and process distal to aperture much shorter than in *Pleistacantha.*

Bothromaia griffini resembles species of *Cyrtomaia* Miers, 1886, in the generally rather smooth inflated carapace with its conspicuous slender spines, though not in the position and relative lengths of the spines, but many other features of *Cyrtomaia* species, such as shape of the carapace and its marginal spination, the rostrum, basal antennal article fused to front, eyes, and shape and dimension of legs, are quite different.

Superfamily Homoloidea de Haan, 1839
Family Poupiniidae Guinot, 1991
Poupinia hirsuta Guinot, 1991
Fig. 5

Material.—USNM 250886, ♂, Commonwealth of the Northern Mariana Islands,

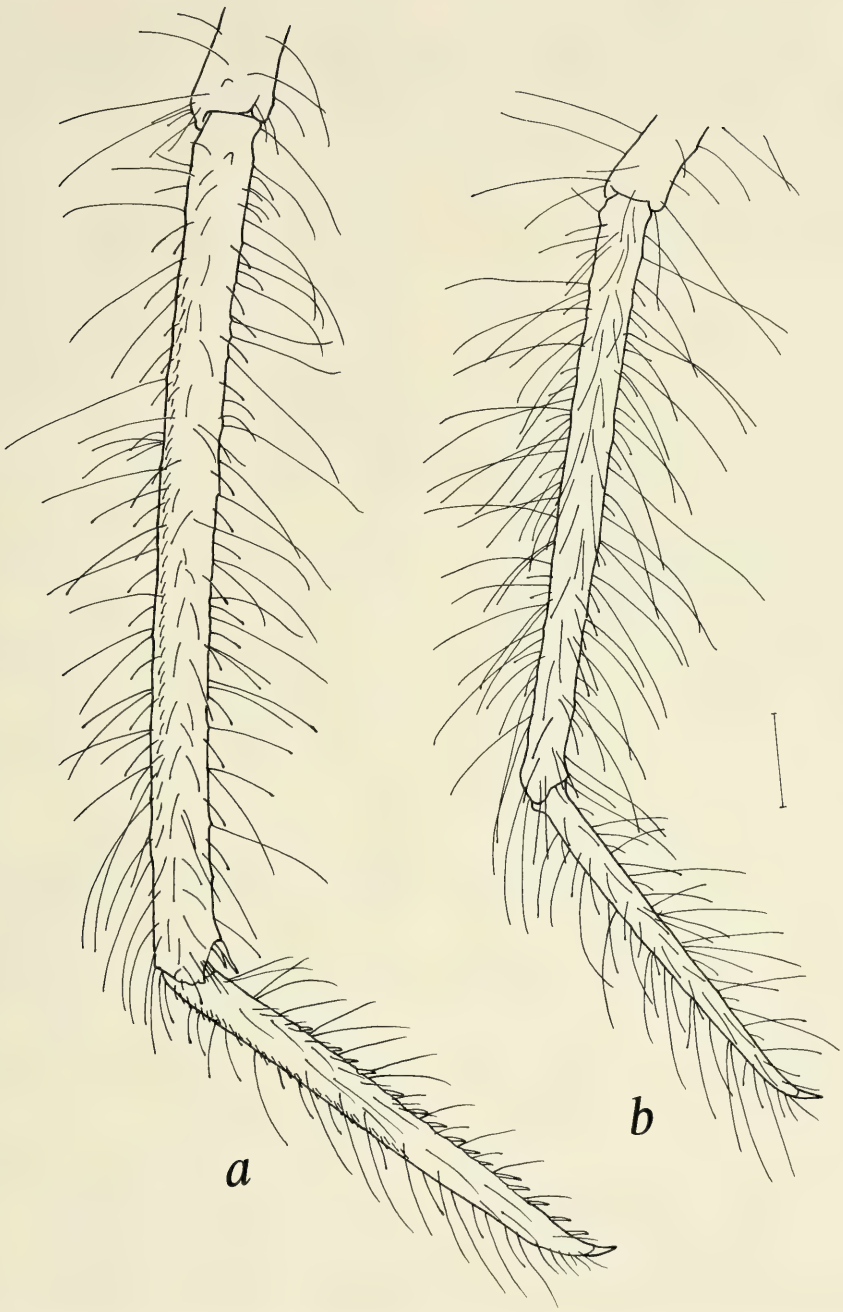


Fig. 5. *Poupinia hirsuta.* Male, semidiagrammatic dorsal view of distal articles on left fourth and fifth legs, ornamentation includes scattered setae with minutely spatulate tips: a, fourth leg with dactyl spined on flexor surface; b, fifth leg with spineless dactyl. Scale = 5 mm.

Table 1.—*Poupinia hirsuta* ♂, length in mm of articles in legs 1–5, right side.

Leg	Merus	Carpus	Propodus	Dactyl	Total
1	19	11	23	~11	53
2	33	28	29	18	108
3	43	23	35	22	123
4	48	20	41	25	135
5	44	16	32	22	114

Arakane Reef, 15°38.2′N, 142°46.3′E, 366–421 m, *Townsend Cromwell* cruise 83–05, sta 152, 16–17 Oct 1983, shrimp trap.

Measurements (*mm*).—Fork length of carapace in midline 33.4, maximum width 29.0; length legs, proximal end of merus to tip of dactyl, cheliped 41, 2nd leg 108, 3d leg 123, 4th leg 135, 5th leg 114.

Remarks.—The adult male specimen reported here is immediately recognizable as the striking homoloid species described by Guinot (1991) from baited trapping at similar depth in the Society Islands. The locality, however, is over 7000 km northwest of Raiatea, suggesting that the distribution of this species is widespread in the tropical southern and western Pacific.

Before establishment of the Poupiniidae, the Homoloidea were characterized as having the fifth legs dorsal in position, reduced, and subchelate or chelate. Discovery of *Poupinia hirsuta,* changes this definition. The new crab has fifth legs that originate in a dorsal position, but their length is intermediate beween that of the first, second, and third ambulatory legs (Table 1). The fifth legs are somewhat more slender than the preceding ambulatory legs, but not subcheliform, and they are less adapted for grasping than their antecedents, for the spineless dactyl does not close against spines on the flexor surface of the propodus, whereas each of the preceding ambulatories has its dactyl spined on the flexor surface, the proximal part of which closes between a pair of movable spines on the distal flexor surface of the propodus. The relatively unmodified and presumably primitive structure of this limb sets the new genus and species apart from all other members of the Homoloidea, which possess variously reduced and specialized subcheliform fifth legs.

The family Homolidae, often attributed to Henderson (1888) who gave the first comprehensive diagnosis, was actually authored by de Haan (1839) (International Commission on Zoological Nomenclature 1987). Alcock (1900, 1901) restricted the family Homolidae when he diagnosed the family Latreilliidae proposed by Stimpson (1858) (International Commission on Zoological Nomenclature 1987). Since then, students of these crabs have viewed the inclusiveness of these families in two ways (Williams 1982). Ihle (1913), Gordon (1950), Monod (1956), Balss (1957), Sakai (1965), and Serène & Lohavanijaya (1973), subsumed the Latreilliidae within the Homolidae. Griffin (1965), Glaessner (1969), Guinot (1979), Eldredge (1980), Guinot & Richer de Forges (1981), and Zarenkov & Khodkina (1981) did not concern themselves with this question, but Rathbun (1937), Wright & Collins (1972), Sakai (1976), Manning & Holthuis (1981), Williams (1982), Wicksten (1985), Melo (1990), and Guinot (1991) agreed with Alcock on distinctiveness of the two families. Collectively, these authors have recognized 38 living species of Homolidae and 9 species of Latreilliidae, although other undescribed species of the latter are known.

Wright & Collins (1972) observed that the essential characteristic distinguishing the Homolidae from the Latreilliidae is presence of the *linea homolica* in the former and its absence in the latter. They considered that other attributes such as number of gills and epipodites, relative lengths of basal and terminal articles of the eyestalks, and the more or less continuous range of carapace shapes, from rectangular (homolids) to acute-angled isosceles triangular (latreilliids), pale into insignificance when presence or absence of the *linea homolica* is

considered. That seemingly essential dichotomy, represented among 25 recognized fossil species in 7 genera collectively summarized by Glaessner (1929, 1969), Wright & Collins (1972), Jenkins (1977), Bishop (1982, 1983, 1986), Takeda & Fujiyama (1983), and Förster & Stinnesbeck (1987), has existed since the early Upper Cretaceous, and was foretold in the Late Jurassic.

Although Wright & Collins (1972) characterized the Homolidae as having long slender legs, except for the reduced and dorsal fifth pair, fossil remains have either no legs preserved, or rare vestiges of them preserved. They described fossil *Homolopsis edwardsii* Bell, for example (paraphrasing, pp. 47–48), as having: chelipeds rather small; merus as long as carapace, longitudinally sulcate and slightly granulate; carpus cuboid; propodus as long as width of orbitofrontal margin; hands as long as wide, and oval in section; fingers slender and as long as or longer than hand. Ambulatory legs long and slender; meri angular in section, granulated and spinous on both borders. Nothing was said of the carpi, propodi, or dactyls, nor was reference made to characters of the fifth legs, but this species apparently offers no evidence to abridge the current family definition. Bishop (1983) figured his *Zygastrocarcinus griesi* with rather stout, coarsely granulated proximal articles on the chelipeds, and ambulatory legs 1, 2, and possibly 3, with rather stout, flattened, sulcate meri, but there is no evidence of the fifth pair of legs, although he did show them as reduced in dorsal position in a reconstruction drawing (fig. 2:901).

The significance of bilateral branchial count in the Homoloidea has received varied interpretation. Alcock (1900, 1901) perceived a clear distinction in branchial count between the Latreilliidae (8 gills and an epipodite on each of the 3 maxillipeds, although he did not analyze the count in *Latreillopsis* which he included in this family) and the Homolidae (14 gills and 6 epipodites, 1 on each of the 3 maxillipeds, the chelipeds, and ambulatory legs 1–2). Gordon (1950) found these differences in branchial count less clear-cut, for there is variation in branchial development among genera that Alcock grouped in the Homolidae, some having only 13 gills and 5 epipodites. Certain gills of some species tend to be reduced as well. *Latreillopsis* has only 10 gills and 4 epipodites, hence is intermediate in this respect between Alcock's standard for latreilliids and homolids. Griffin (1965) concurred that branchial count may be an unreliable character that needs further study. Still, latreilliids seem to be characterized by an essentially triangular carapace lacking the *linea homolica,* 8 gills and 3 epipodites, and fifth legs reduced and dorsal. Homolids have a subrectangular or ovoid carapace with *linea homolica,* 10 to usually 14 gills, 4 to usually 6 epipodites, and fifth legs reduced and dorsal.

The branchial formula of *Poupinia hirsuta* is incompletely known. Guinot (1991) observed epipodites on the first three legs, but possibly was reluctant to dissect rare perfect specimens to determine the full branchial formula, as are we. As a substitute for dissection, radiographs of our specimen indicate epipodites on maxilliped 3, the cheliped, and ambulatory legs 1–2. Faint outlines of gills seem to be evident on somites associated with maxilliped 3, the cheliped, and ambulatory legs 1–3, but the actual gill count cannot be ascertained from these images. The images indicate that the count may conform with that of the Homolidae rather than the Latreilliidae, or lie between these extremes.

Poupinia hirsuta, in the Poupiniidae, thus bridges these two groups in that it has an ovoid carapace with no *linea homolica,* epipodites on maxilliped 3, chelipeds, and ambulatory legs 1–2 (based on radiographs), seems to have a high gill count, and fifth legs normal in size, the most primitive condition, though originating in dorsal position. The suite of characters is set forth in the following:

Key to Families of Homoloidea

1. *Linea homolica* present .. Homolidae
– *Linea homolica* absent 2
2. Carapace ovate in dorsal outline, anterior part not extended into "neck" and prominent rostral horns; leg 5 normal, neither subchelate nor conspicuously diminished in length ..... Poupiniidae
– Carapace sub-isosceles-triangular in dorsal outline, anterior part extended into "neck" and prominent divergent rostral horns; leg 5 conspicuously diminished in length, usually subchelate ..... Latreilliidae

Acknowledgments

We are indebted to B. Burch (BPBM), L. G. Eldredge, Pacific Science Association, Honolulu, P. Davie (QM), and D. J. G. Griffin, J. K. Lowry, and P. B. Berents (AMS) for access to the crustacean research collections in their institutions, and for many courtesies. C. Clark and W. C. Blow assisted with photography, M. Nizinski assisted with radiography, and the drawings were inked by Keiko Hiratsuka Moore. We thank G. A. Bishop, F. A. Chace, Jr., B. B. Collette, and R. B. Manning for reading the manuscript.

Literature Cited

Alcock, A. 1900. Materials for a carcinological fauna of India. No. 5. The Brachyura Primigenia or Dromiacea.—Journal Asiatic Society of Bengal 68(2), No. 3:123–169.

———. 1901. Catalogue of the Indian decapod Crustacea in the collection of the Indian Museum. Part I. Brachyura. Fasciculus I. Introduction and Dromides or Dromiacea (Brachyura Primigenia). Calcutta, Printed by order of the Trustees of the Indian Museum, ix + 80 pp., plates A & 1–8.

Balss, H. 1957. Decapoda. VIII. Systematik. Dr. H. G. Bronn's Klassen und Ordnungen des Tierreichs. Bd. 5, Abt. 1, B. 7, Lf. 12:1505–1672, Leipzig, Akademische Verlagsgesellschaft, Geest & Portig K.-G.

Bate, C. S. 1888. Report on the Crustacea Macrura collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76 . . . etc. Zoology 24, xc + 942 pp., 150 plates.

Bishop, G. A. 1982. *Homolopsis mendryki*: a new fossil crab (Crustacea, Decapoda) from the Late Cretaceous *Dakoticancer* Assemblage, Pierre Shale (Maastrichtian) of South Dakota.—Journal of Paleontology 56:221–225.

———. 1983. Two new species of crabs, *Notopocorystes (Eucorystes) eichhorni* and *Zygastrocarcinus griesi* (Decapoda: Brachyura) from the Bearpaw Shale (Campanian) of north-central Montana.—Journal of Paleontology 57:900–910.

———. 1986. A new crab, *Zygastrocarcinus cardsmithi* (Crustacea, Decapoda), from the Lower Pierre Shale, southeastern Montana.—Journal of Paleontology 60:1097–1102.

Eldredge, L. G. 1980. Two species of *Homola* (Dromiacea, Homolidae) from Guam.—Micronesica 16:271–277.

Förster, R., & W. Stinnesbeck. 1987. Zwei neue Krebse, *Callianassa saetosa* n. sp. und *Homolopsis chilensis* n. sp. (Crustacea, Decapoda) aus der Oberkreide Zentral-Chiles.—Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 27:51–65.

Glaessner, M. F. 1929. Crustacea Decapoda. Fossilium Catalogus. 1. Animalia, Pars 41:1–464, W. Junk, Berlin.

———. 1969. Decapoda. Pp. R399–R533, R626–R628 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, Pt. R, Arthropoda 4, Vol. 2. The Geological Society of America, Inc., and The University of Kansas.

Gordon, I. 1950. Crustacea Dromiacea. Part I. Systematic account of the Dromiacea collected by the "John Murray" Expedition. Part II. The morphology of the spermatheca in certain Dromiacea.—The John Murray Expedition, 1933–34, Scientific Reports, Vol. 9, Zoology and Botany:201–253, 1 plate.

Griffin, D. J. G. 1965. A new species of *Paromola* (Crustacea, Decapoda, Thelxiopidae) from New Zealand.—Transactions of the Royal Society of New Zealand 7(4):85–91, 2 plates.

———, & H. A. Tranter. 1986. The Decapoda Brachyura of the Siboga Expedition, Part VIII, Majidae.—Siboga-Expeditie Monographie 39, C4:1–335, 22 plates.

Guinot, D. 1979. Morphologie et phylogenèse des brachyoures.—Mémoires du Muséum National d'Histoire Naturelle, New Series, Series A, Zoologie 112:1–354, 27 plates.

———. 1985. Crabes bathyaux de l'Île de la Réunion; description de *Cyrtomaia guillei* sp., nov., de *Platypilumnus inermis* sp. nov. et de *Psopheti-*

cus vocans sp. nov. (Crustacea Decapoda Brachyura). Résultats de Campagnes Océanographiques du M.S. "Marion-Dufresne" et de Prospections Littorales de la Vedette "Japonaise."—Comité National Française de Recherches Antarctiques, No. 55 (for 1984):7–31, plates 1–4.

———. 1991. Établissement de la famille des Poupiniidae pour *Poupinia hirsuta* gen. nov., sp. nov. de Polynésie (Crustacea Decapoda Brachyura Homoloidea).—Bulletin du Muséum National d'Histoire Naturelle, Paris, Sér. 4, 12A(3-4, for 1990):577–605.

———, & B. Richer de Forges. 1981. Homolidae, rares ou nouveaux, de l'Indo-Pacifique (Crustacea, Decapoda, Brachyura).—Bulletin du Muséum National d'Histoire Naturelle, Paris, Sér. 4, 3A(2):523–581.

———, & ———. 1982a. Nouvelles récoltes des genres *Cyrtomaia* Miers et *Pleistacantha* Miers (Crustacea, Decapoda, Brachyura).—Bulletin du Muséum National d'Histoire Naturelle, Paris, Sér. 4, 3A(4, for 1981):1087–1125.

———, & ———, 1982b. Révision du genre Indo-Pacifique *Cyrtomaia* Miers, 1886: Campagnes océanographiques du *Challenger,* de l'*Albatross,* du *Siboga* et du *Vauban* (Crustacea Decapoda Brachyura).—Annales de l'Institut Océanographique, N. S. 58, Fasc. 1:5–88.

———, & ———. 1985. Crustacés, Décapodes: Majidae (genres *Platymaia, Cyrtomaia, Pleistacantha, Sphenocarcinus* et *Naxioides*). Résultats des Campagnes Musorstom I et II, Philippines (1976, 1980), Vol. 2.—Mémoires du Muséum National d'Histoire Naturelle, Paris, Sér. A, 133, Zoologie (I & II. Philippines), 4:83–176, 11 plates.

de Haan, W. 1839 Crustacea. *In* P. F. von Siebold, Fauna Japonica sive descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorium, qui summum in India Batavia imperium tenent, suscepto, annis 1832–1830 collegit, notis observationibus et adumbrationibus illustravit, fasc. 4:73–108, plates 25–32, G, H.

Henderson, J. R. 1888. Report on the Anomura collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76 . . . etc., Zoology 27(69):i–xi, 1–221, 21 plates.

Ihle, J. E. W. 1913. Die Decapoda Brachyura der Siboga-Expedition. I, Dromiacea.—Siboga-Expeditie, Monographie 39*b*:1–96, 4 plates.

International Commission on Zoological Nomenclature. 1987. Official lists and works in zoology. R. V. Melville & J. D. D. Smith (eds.). The International Trust for Zoological Nomenclature, c/o British Museum (Natural History), London, 366 pp.

Jenkins, R. J. F. 1977. A new fossil homolid crab (Decapoda, Brachyura), Middle Tertiary, southeastern Australia.—Transactions of the Royal Society of South Australia 101:1–10.

MacLeay, W. S. 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. Pp. 53–71, plates 2, 3 *in* Illustrations of the Annulosa of South Africa . . . etc.; fitted out by The Cape of Good Hope Association for Exploring Central Africa, London.

Manning, R. B., & L. B. Holthuis. 1981. West African brachyuran crabs (Crustacea: Decapoda).—Smithsonian Contributions to Zoology 306:i–xii, 1–379.

Melo, G. A. S. de. 1990. Descrição de *Latreillia williamsi,* sp. n. (Crustacea, Brachyura, Homoloidea), e a occorrẽcia da familia Latreilliidae no litoral Brasileiro.—Atlántica, Rio Grande:12(2): 27–34.

Miers, E. J. 1879. On a collection of Crustacea made by Capt. H. C. St. John, R.N., in the Corean and Japanese seas. Part I. Podophthalmia. With an appendix by Capt. H. C. St. John.—Proceedings of the Zoological Society of London, pp. 18–61, 3 plates.

———. 1886. Report on the Brachyura collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76 . . . etc., Zoology 17(49):i–1, 1–362, 29 plates.

Moffitt, R. B., & J. J. Polovina. 1987. Distribution and yield of the deepwater shrimp *Heterocarpus* resource in the Marianas.—Fishery Bulletin, U.S. 85(2):339–349.

Monod, T. 1956. Hippidea et Brachyura ouest-africains.—Mémoires de l'Institut Français d'Afrique Noire 45:1–674.

Polovina, J. J., R. B. Moffitt, S. Ralston, P. M. Shiota, & H. A. Williams. 1985. Fisheries resource assessment of the Mariana Archipelago, 1982–85.—Marine Fisheries Review 47(4):19–25.

Rathbun, M. J. 1937. The oxystomatous and allied crabs of America.—United States National Museum Bulletin, 166:i–vi, 1–278, 86 plates.

Richer de Forges, B., & D. Guinot. 1988. Description de trois espéces de *Cyrtomaia* Miers, 1886, de Nouvelle-Calédonie et des Iles Chesterfield (Crustacea Decapoda Brachyura).—Bulletin du Muséum National d'Histoire Naturelle, Paris, Sér. 4, 10A(1):39–55.

Sakai, T. 1965. The crabs of Sagami Bay. East-West Center Press, Honolulu, Hawaii, xvi + 200 pp. (English text), 100 plates, 92 pp. (Japanese text), 32 pp. (Bibliography and Indexes).

———. 1976. Crabs of Japan and the adjacent seas. Kodansha Ltd., Tokyo, 773 pp. (English text), 251 plates, 461 pp. (Japanese text).

Samouelle, G. 1819. The entomologist's useful com-

pendium, or an introduction to the knowledge of British insects . . . etc. Printed for Thomas Boys, London, 496 pp.

Serène, R., & P. Lohavanijaya. 1973. The Brachyura (Crustacea: Decapoda) collected by the Naga Expedition, including a review of the Homolidae.—Naga Report 4(4):1–187, 21 plates.

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Crustacea Anomoura.—Proceedings of the Academy of Natural Sciences of Philadelphia 10(7):225–252.

Takeda, M., & I. Fujiyama. 1983. Three decapod crustaceans from the Lower Cretaceous Miyako Group, northern Japan.—Bulletin of the National Science Museum, Series C (Geology & Paleontology) 9(4):129–136, 2 plates.

Wicksten, M. K. 1985. Carrying behavior in the family Homolidae (Decapoda: Brachyura).—Journal of Crustacean Biology 5(3):476–479.

Williams, A. B. 1982. Revision of the genus *Latreillia* Roux (Brachyura: Homoloidea).—Quaderni del Laboratorio de Tecnologia della Pesca, Ancona, Italy 3(2–5):227–255.

Wright, C. W., & J. S. H. Collins. 1972. British Cretaceous crabs.—Palaeontographical Society Monographs 126(533):1–114, 22 plates.

Zarenkov, N. A., & I. V. Khodkina. 1981. Decapod crustaceans. Pp. 83–93, 154 *in* A. P. Kusnetsov & A. N. Mironov, eds., Benthos of the submarine mountains Marcus-Necker and adjacent Pacific regions. Academy of Sciences of the USSR, P.P. Shirshov Institute of Oceanology, Moscow. [In Russian.]

(ABW) National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, (RBM) National Marine Fisheries Service, Southwest Fisheries Science Center Honolulu Laboratory, 2570 Dole Street, Honolulu, Hawaii 96822-2396.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 583–592

TWO NEW SPECIES OF *NETAMELITA* FROM THE CARIBBEAN SEA (CRUSTACEA: AMPHIPODA: GAMMARIDEA)

James Darwin Thomas and J. L. Barnard

Abstract.—The previously described species of *Netamelita* from California and the Gulf of Mexico are reviewed and two new species, *N. brocha* and *N. tabaci,* are described from the Florida Keys and Belize, respectively. A key to the species of *Netamelita* is provided. In the Caribbean Sea these species live on fine coralgal muds in forereef environments at depths of 30–40 m in a distinctive amphipod assemblage dominated by the genera *Garosyrrhoe* and *Metaceradocus.* The two new species of *Netamelita* were observed to plough through fine surficial flocculent materials, head downward, with urosomal appendages elevated above the sediment surface.

Our revision of *Netamelita* includes an emended diagnosis of the genus which formerly included only the type-species. Four species are now assigned to this genus; the revision below, with listing of species, references and biogeographic codes in brackets, reflects the format of Barnard and Barnard (1983).

New observations on the type-species, *N. cortada,* are given from our examination of the original material, courtesy of Dr. Joel L. Martin, Los Angeles County Museum.

Psammomelita uncinata Vonk (1988), an interstitial genus and species from coral sands of Curacao differs from *Netamelita* in the unique presence of hooks emerging from the sterna of pleonites 1–3 on the medial sides of the pleopods, a curved keel on the male maxillipeds, and a weaker lobe on the carpus of gnathopod 2. A fourth difference cited by Vonk, presence of heavy serrations on article 2 of pereopods 5–7, is now abandoned because that character is present in our new species of *Netamelita.*

Netamelita J. L. Barnard, 1962

Netamelita J. L. Barnard, 1962:110 (*Netamelita cortada* J. L. Barnard, 1962, original designation).

Diagnosis.—Body subvermiform. Rostrum absent. Lateral cephalic lobes rounded, sinus absent or very weak. Eyes moderately developed.

Antenna 1 elongate, longer than half of body length, ratio of peduncular articles = 20:15:4; primary flagellum slightly longer than peduncle; accessory flagellum 1-articulate. Antenna 2 short, about half as long as antenna 1, article 5 shorter than 4, flagellum shorter than peduncle, with about 7–8 articles.

Epistome unproduced, upper lip entire. Mandibular raker spines 4 or fewer, ratio of palp articles varying between 7:13:11 and 4:13:15, palp feeble, article 3 linear, setae = E 2–3. Inner lobes of labium fleshy, well developed. Maxillae inner plates naked medially; inner plate of maxilla 1 subrectangular, with 2 (rarely 3) large apical setae and 2 small apicolateral setules, outer plate with 9 spines, palps symmetrical. Inner plate of maxilla 2 without medial setae (often with sparse hair-like scales). Maxilliped lacking keel, inner plate bearing only apical setae, outer plate with medial spines, article 3 of palp lobed or unlobed, dactyl shorter than 3, unguiform, with nail.

Coxae short, scarcely touching or significantly overlapping, coxa 1 with subangular

anteroventral corner, in most species curved forward; coxa 4 unlobed, scarcely longer than coxa 5.

Gnathopods 1–2 feeble, mittenform, of similar size, carpi elongate, propodi shorter or scarcely shorter than carpi, rectangular, palms slightly oblique, short, carpus of gnathopod 1 unlobed, of gnathopod 2 well lobed.

Pereopods 5–7 progressively longer but together not greatly elongate. Article 2 of pereopods 5–6 alike, weakly to moderately expanded, of pereopod 7 expanded, lobate or not (type).

Outer rami of uropods 1–2 not significantly shortened or outer ramus of uropod 2 shortened, uropod 1 with basofacial spine; uropods 1–2 usually with 1 or more long displaced apical spine(s) on peduncle; uropod 3 greatly extended, parviramous, outer ramus elongate, primarily 1-articulate, with microscopic article 2. Telson of ordinary length, almost fully cleft, with weak or strong apical armaments, any penicillate setae apicad.

Coxal gills 2–6, thinly ovate, not stalked; oostegites very narrow, poorly setose (data from 3 species cited herein).

Relationship.—*Psammomelita* differs from *Netamelita* in the unique presence of hooks emerging from the sterna of pleonites 1–3 on the medial sides of the pleopods, and a curved keel on the male maxillipeds. Epimeron 1 has a giant anteroventral spine but this is present in one of our two species of *Netamelita.* Article 2 of pereopods 5–7 has large posterior serrations but both of our new species have that character. The carpus of gnathopod 2 is poorly produced but this is also true of our species. The latter three characters therefore are no longer diagnostic of *Psammomelita.*

A transformation of characters between the California type species of *Netamelita* and the Caribbean *Psammomelita* occurs in our new Caribbean species of *Netamelita* in the condition of epimeron 1, gnathopod 2, and pereopods 5–7. *Psammomelita* has 2 additional apomorphic characters, the pleonosternal hooks and keel on the maxillipeds. This does not necessarily mean that we consider the California *N. cortada* to have the plesiomorphic condition for all of the characters mentioned. It is very possible that *N. cortada* has lost what appear to be apomorphic characters in *Psammomelita* and Caribbean *Netamelita,* and thus has lost pleopodal hooks, anteroventral spine and protrusion of epimeron 1, and pereopodal serrations, while retaining what we consider to be the plesiomorphic (via *Eriopisella*) carpus of gnathopod 2.

Species.—*Netamelita barnardi* McKinney et alia, 1978, Texas [474]; *N. brocha* Thomas & Barnard, herein, Florida [478]; *N. cortada* J. L. Barnard, 1962, NE Pacific warm-temperate [370]; *N. tabaci* Thomas & Barnard, herein, Yucatan region [471].

Distribution.—Marine, California, Caribbean Sea, 15–76 m, 4 species.

Key to the Species of *Netamelita*

1. Article 2 of pereopods 5–7 with large serrations, main spine on telson at least ⅔ length of telson 2
– Article 2 of pereopods 5–7 with tiny or no serrations, main spine on telson less than ⅛ length of telson .. 4
3. Article 2 of pereopod 7 not lobate, epimeron 1 without thick anteroventral spine ..... *N. brocha*
– Article 2 of pereopod 7 lobate, epimeron 1 with thick anteroventral spine ..... *N. tabaci*
4. Article 2 of pereopod 7 with some long posterior setae 1.5 times length of article 3, anteroventral lobe of coxa 1 longer than width of coxa at base, epimeron 3 with ventral spines as long as any spine on uropods 1–3 ..... *N. barnardi*
– Article 2 of pereopod 7 with long posterior setae less than 0.5 times length of article 3, length of anteroventral lobe of coxa 1 less than half

width of coxa at base, epimeron 3 with ventral spines less than one third as long as any spine on uropods 1–3 ..... *N. cortada*

Netamelita cortada J. L. Barnard

Netamelita cortada J. L. Barnard, 1962:113, fig. 23.

Diagnosis.—Coxa 1 moderately curved forward. Article 2 of pereopods 6–7 weakly lobed posteroventrally, of 5–7 smooth to very minutely serrate. Epimeron 1 without posteroventral tooth, without thick anteroventral spine; epimera 2–3 each with small simple posteroventral tooth, epimeron 2 bearing dense ventral setae, epimeron 3 with 6 small ventral spines. Outer ramus of uropod 1 scarcely shortened, of uropod 2 strongly shortened, lacking marginal spine. Peduncle of uropod 2 without huge spine. Apical spines of telson very short, less than one-fifth as long as telson.

Subsidiary observations.—Based on reexamination of holotype now in Los Angeles County Museum. Article 1 of mandibular palp slightly elongate, without seta, article 2 naked, article 3 with 2 apical setae. Right lacinia mobilis with 3 teeth, left with 4 teeth. Left mandible with 1 large and 2 small rakers, right with 2 large and 2 small rakers. Outer plate of maxilla 1 with 9 spines. Inner plate of maxilliped with 11 apical setae, 1 coupling spine, no medial or mediofacial setae; outer plate with 5 long apical comb-setae, 9 medial spines and pairs or triads of medioventral shorter simple spines totaling 13 spines; palp article 3 expanded and produced, pubescent. Coxa 7 lacking gill. Epimeron 1 lacking anteroventral spine. Sterna of pleosome lacking triangular projections or hooks. Peduncle of uropod 1 with basofacial spine, with apical displaced spines, lateral one of medium size, medial one of large size, lateral and medial apex also with small partner spine(s). Peduncle of uropod 2 with 2 dorsolateral spines in tandem, with small lateral and medial displaced spines, plus 2 sets of more proximal medial spines in tandem. Rami of uropod 1 with 3(?4) apical spines, inner with one marginal spine; of uropod 2 each ramus with 5 apical spines, outer with no marginal and inner with 2 and 3 opposite marginal spines. Apex of each telsonic lobe with one short spine, one or two apical penicillate setules and pair of lateral penicillate setules near apex.

Material examined.—The holotype in the Los Angeles County Museum (now owner of collections from Allan Hancock Foundation).

Distribution.—Southern California between Point Conception and Gaviota, 20 m.

Netamelita brocha, new species
Figs. 1–3 (part)

Etymology.—From Latin, *brochus,* toothed, referring to the teeth of the pereopods.

Diagnosis.—Coxa 1 strongly curved forward. Article 2 of pereopods 5–7 not lobed posteroventrally, of 5 weakly serrate, of 6 moderately serrate, of 7 strongly serrate. Epimera 1–3 each with sharp posteroventral tooth, tooth doubled on epimeron 1, epimeron 1 lacking thick anteroventral spine, epimeron 2 with several ventral and subfacial setae; epimeron 3 with row of ventral marginal spines (6 in holotype). Outer rami of uropods 1 and 2 not shortened, with marginal spine(s). Peduncle of uropod 2 with 1+ huge spine. One apical spine of telson at least three-quarters as long as telson.

Subsidiary observations.—Article 1 of mandibular palp short, with one seta, article 2 naked, article 3 with 3 apical setae. Left and right mandibles with 2 rakers. Maxilla 1 outer plate with 9 spines, palp article 2 with 9 apical elements. Maxilliped outer plate with 5–6 long apical comb-setae, and pairs or triads of medioventral shorter simple spines, palp article 3 expanded, lobate apicolaterally. Uropod 1 peduncle with apical displaced spines, lateral one of medium

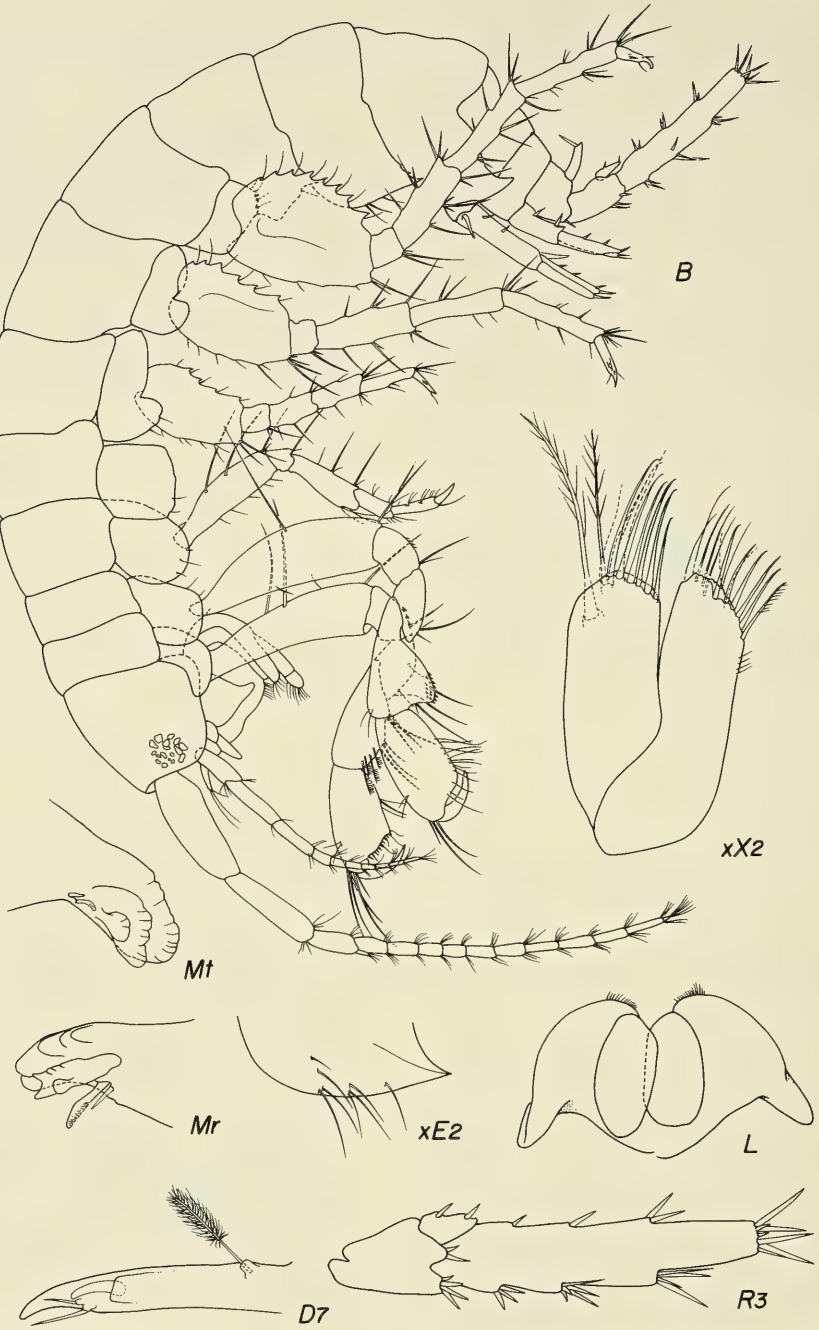


Fig. 1. *Netamelita brocha,* n. sp., figures without lower case letter to left of each caption = holotype male "z," 3.46 mm; x to left of each caption = female "x" 3.45 mm. xE2 is left sided. capital letters in figures refer to parts; lower case letters to left of capital letters refer to specimens and to the right refer to adjectives as described: B, body; C, coxa; D, dactyl; E, epimeron(a); G, gnathopod; H, head; I, inner plate or ramus; L, labium; M, mandible; P, pereopod; R, uropod; S, maxilliped; T, telson; U, upper lip; V, palp; W, pleon; X, maxilla; a, apex; r, right; t, left.

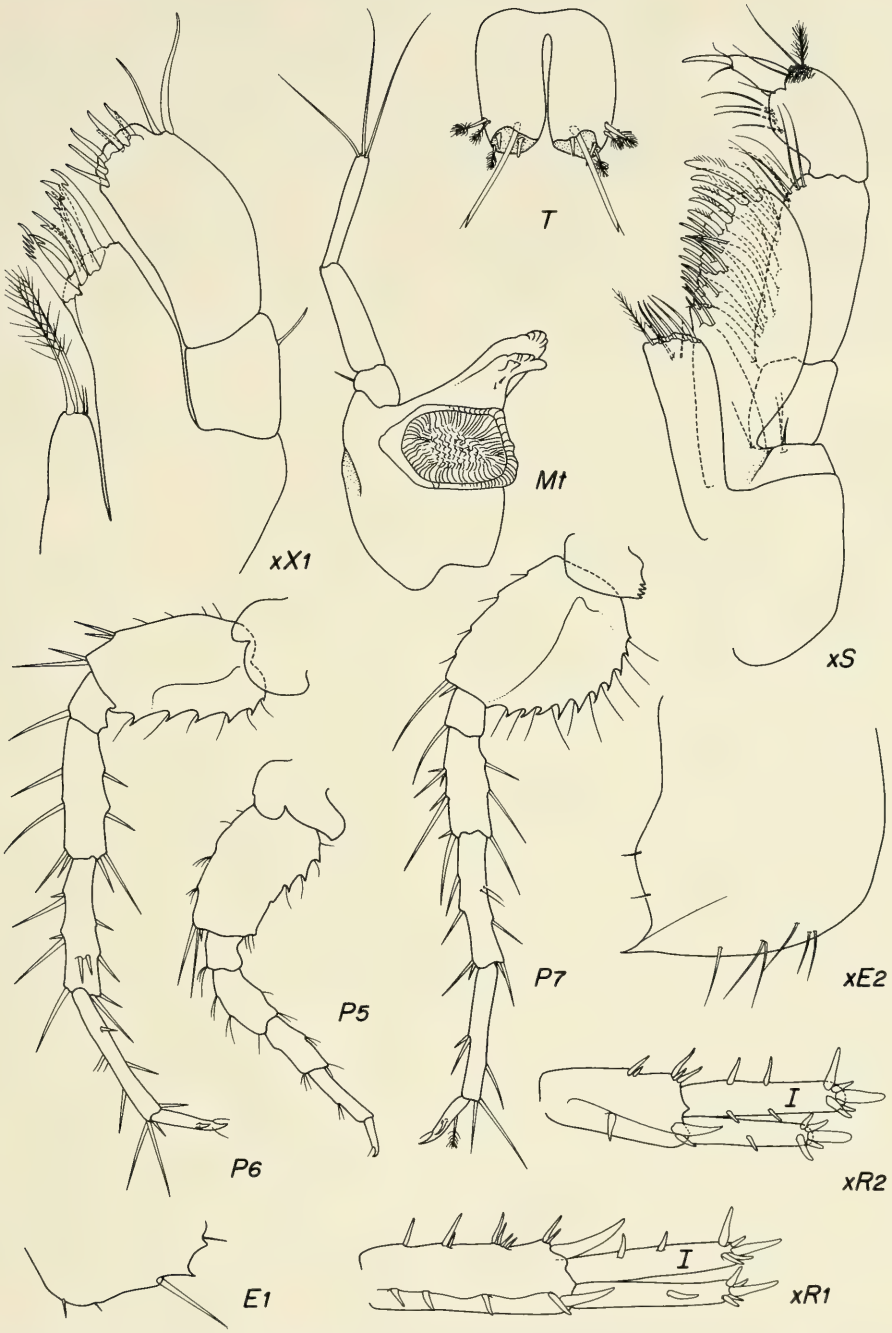


Fig. 2. *Netamelita brocha,* n. sp., figures without lower case letter to left of each caption = holotype male "z," 3.46 mm; x to left of captions = female "x" 3.45 mm. xE2 is right sided.

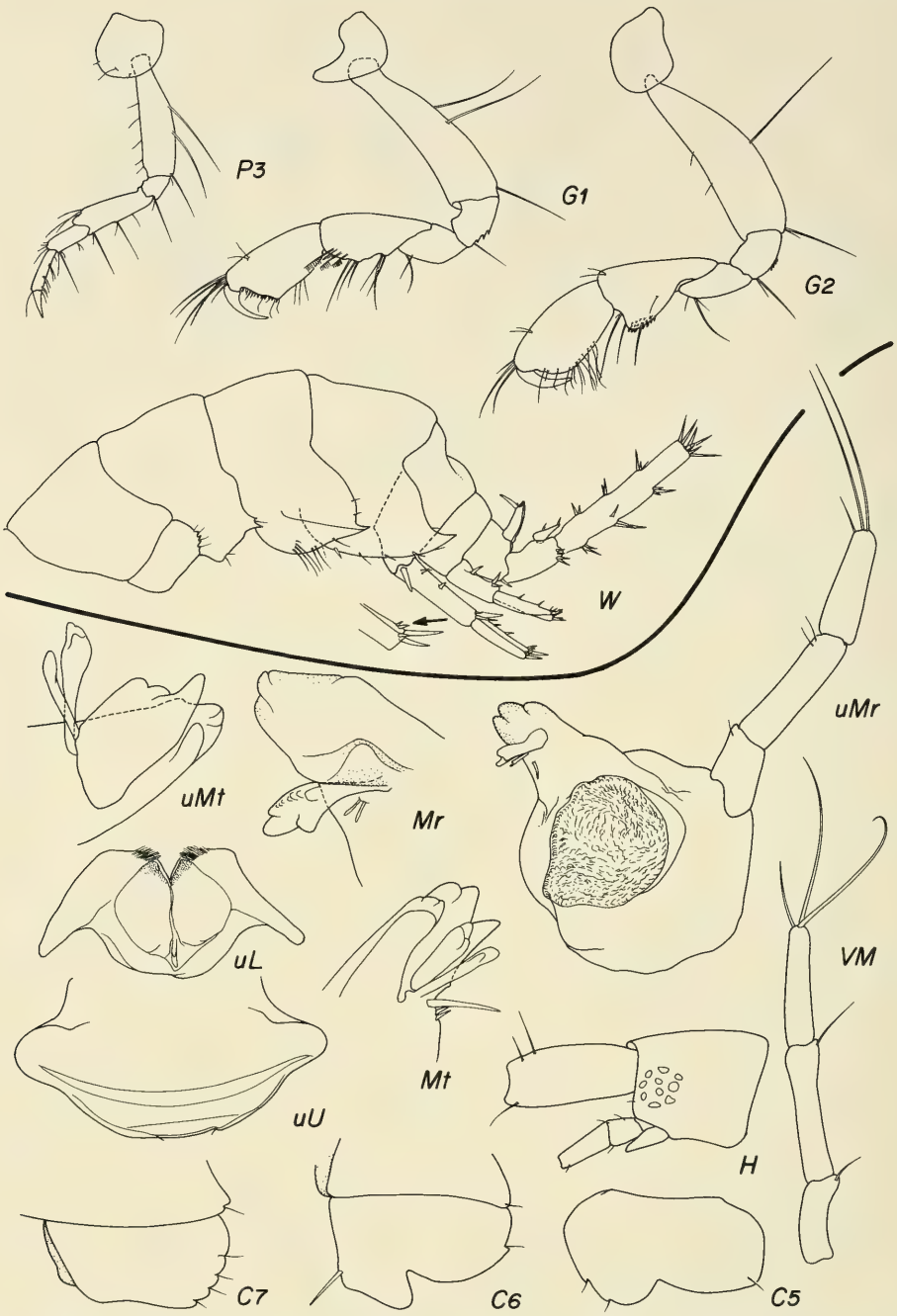


Fig. 3. Upper, *Netamelita brocha,* n. sp., figures without lower case letter to left of each caption = holotype male "z," 3.46 mm; x to left of caption = female "x" 3.45 mm. Lower, *Netamelita tabaci,* n. sp., figures without lower case letter to left of each caption = holotype male "t" 2.58 mm; u to left of caption = female "u" 2.55 mm.

size, medial one of large size, lateral apex also with small partner spine. Uropod 2 peduncle with 2 dorsolateral spines in tandem, with large medial displaced spine and small partner, plus 2 pairs of more proximal medial spines in tandem. Outer and inner rami of uropod 1 with 4 apical spines and one marginal spine; of uropod 2 each ramus with 5 apical spines, outer with no marginal and inner with 2 marginal spines; inner ramus of uropod 3 with 2 spines. Apex of each telsonic lobe with one long spine at least three-fourths as long as lobe, with 2 very short spines, one apicolateral penicillate setule and pair of lateral penicillate setules near apex.

Female "x."—Epimeron 2 with 6 ventral and partly facial setae, 4 of these in 2 pairs; epimeron 3 with 6 ventral spines; outer rami of uropods 1–2 with 1 marginal, inner with 2 marginal spines.

Holotype.—USNM No. 253532, male "z" 3.46 mm.

Type locality.—Florida Keys, 0.25 mi SW of Looe Key Reef, 24°31.20′N, 81°25.93′W, 14 Aug 1978, 35 m, bottom dredge on coralgal mud and large *Halimeda* flakes, coll. J. D. Thomas.

Paratypes.—USNM 253533, type locality, female "x" 3.45 mm; female "y" 3.39 mm; and 12 other specimens; 3 mi S of Looe Key Reef, 9 Aug 1978, 76 m, coralgal mud, 35 specimens; 2 mi S of Looe Key Reef, 4 Jul 1978, 46 m, muddy sand, 3 specimens; same, 30 Sep 1978, 61 m, mixed mud and sand, 1 specimen; 1 mi S of Looe Key Reef, 17 Jul 1978, depth unknown, muddy sand (all samples coll. by J. D. Thomas).

Relationship.—See *N. tabaci.*

Distribution.—Florida Keys, off Big Pine Key, region of Looe Key Reef, 35–76 m.

Netamelita tabaci, new species
Figs. 3–5 (part)

Etymology.—From new Latin *tabacum,* Aboriginal American, referring to the Tobacco Reef Range in Belize, on which the type-locality occurs.

Diagnosis.—Coxa 1 moderately curved forward. Article 2 of pereopods 5–6 not lobed posteroventrally, of 7 strongly lobate, of 5 weakly serrate, of 6 moderately serrate, of 7 strongly serrate. Epimeron 1 with thick anteroventral spine. Epimeron 2 with dense ventral setae. Outer rami of uropods 1 and 2 not shortened, lacking marginal spine. Peduncle of uropod 2 with 1+ huge spine. In male one apical spine of telson at least one-half as long as telson.

Subsidiary observations.—Unlike *N. brocha,* head in both sexes with weak sinus for reception of antenna 2. Article 1 of mandibular palp short, with one seta, article 2 with 2 setae, article 3 with 2–3 apical setae. Left mandible in male with one large multifid raker, one large simple raker and 2 tiny rakers, female similar but lacking two tiny rakers, right mandible in male with 2 tiny rakers, in female none. Outer plate of maxilla 1 with 9 spines, apex of palp article 2 with 7 elements. Outer plate of maxilliped with 6 long apical comb-setae, and pairs or triads of medioventral shorter simple spines, palp article 3 expanded, lobate apicolaterally. Peduncle of uropod 1 with apical displaced spines, lateral one of medium size, medial one of large size, both apices also with small partner spine, apicolateral margin with 2 spines (plus basofacial spine also shown in illustration), medial margin with 3 medial spines in 2 sets. Peduncle of uropod 2 with pair of apicodorsal spines, with large medial displaced spine and no partner. Outer and inner rami of uropod 1 with 4–5 apical spines and zero and one marginal spine; of uropod 2 each ramus with 4 apical spines, outer with no marginal and inner with 1 marginal spine. Inner ramus of uropod 3 with 1 spine. Apex of each telsonic lobe in male with one long spine at least half as long as lobe, with 2 very short spines, one apicolateral penicillate setule and pair of lateral penicillate setules near apex; in

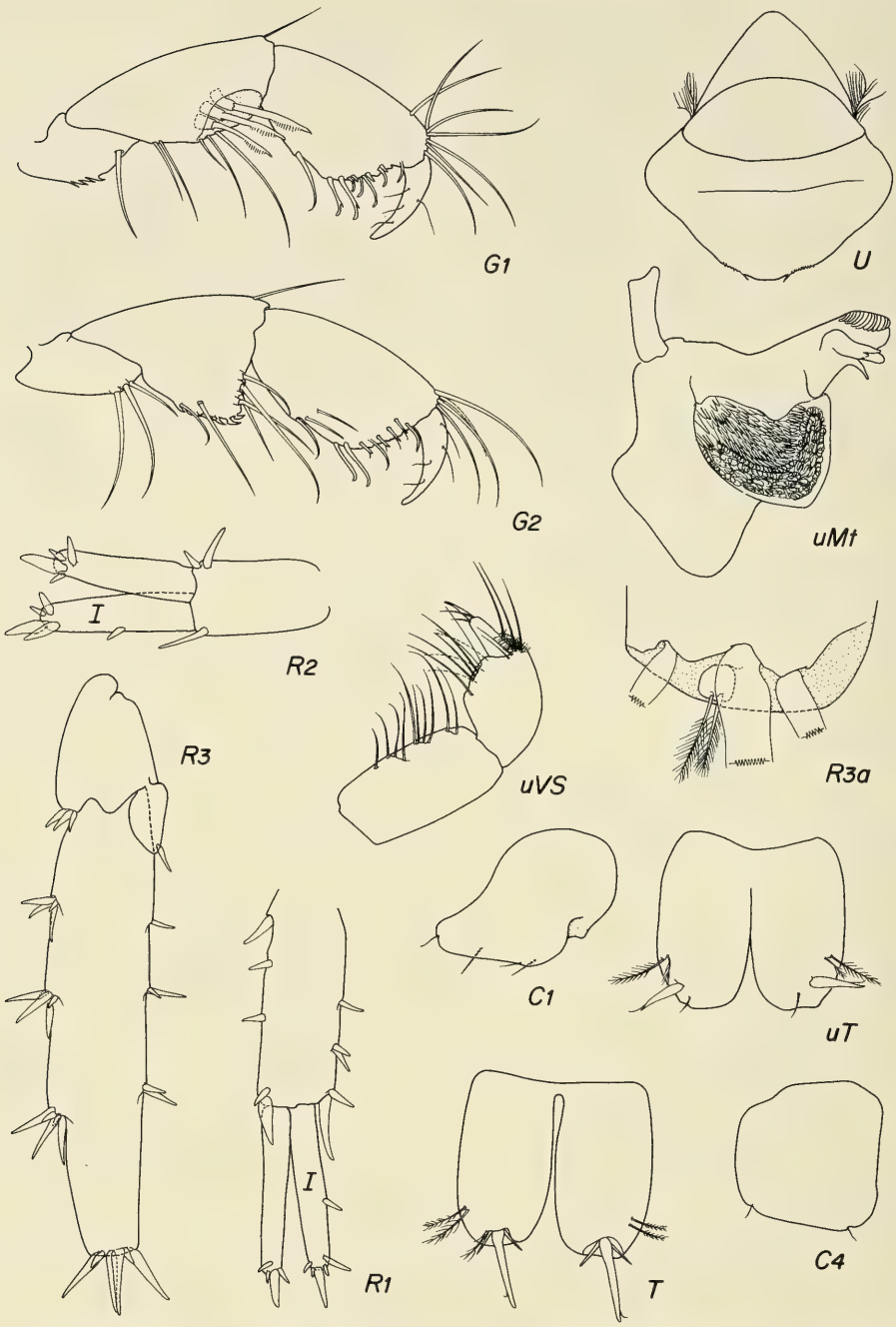


Fig. 4. *Netamelita tabaci,* n. sp., figures without lower case letter to left of captions = holotype male "t" 2.58 mm; u to left of caption = female "u" 2.55 mm.

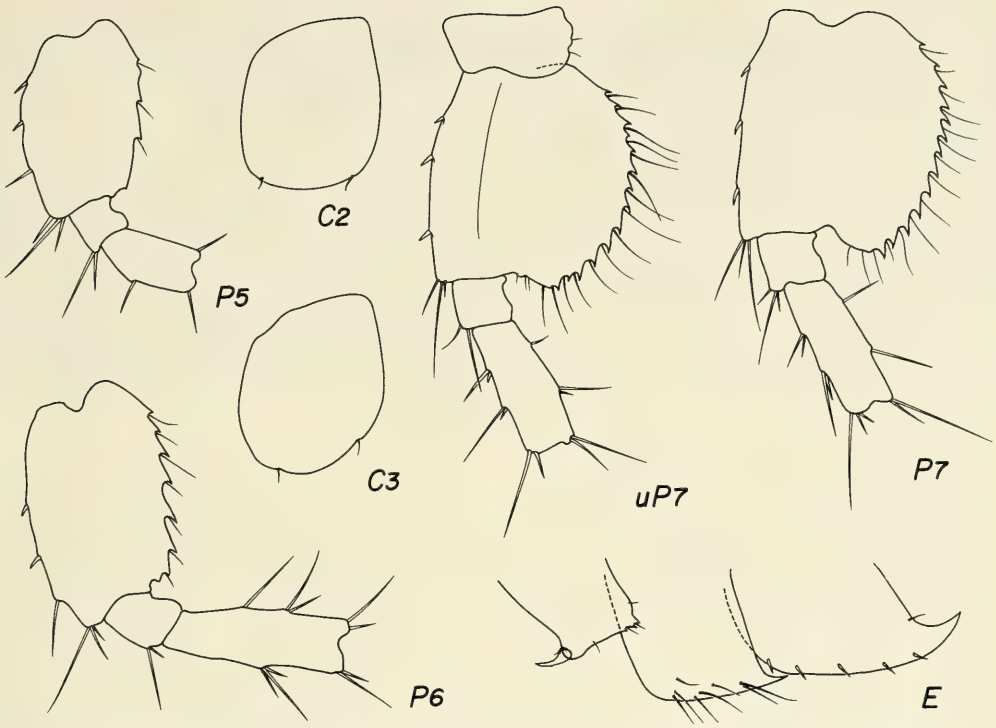


Fig. 5. *Netamelita tabaci,* n. sp., figures without lower case letter to left of caption = holotype male "t" 2.58 mm; figures with u to left of caption = female "u" 2.55 mm.

female main spine only one-fourth as long as telson, other elements fewer (see illustration).

Female "u."—Gills broadly comma-shaped, large on coxa 2, less than one-fourth size on coxa 6; oostegites very thin, sparsely setose. Epimeron 1 with 1 ventral and 1 posteroventral tooth, epimeron 2 with 2-2-1 setae (anterior to posterior), epimeron 3 with 3 ventral spines.

Holotype.—USNM No. 253534, male "t" 2.58 mm.

Type locality.—JDT-BEL-19, Belize, Carrie Bow Key, 16°48′N, 88°05′W, 16 Jun 1979, sand trough in forereef, 29 m, coralgal mud and *Halimeda* flakes, coll. J. D. Thomas.

Paratypes.—Type locality, USNM No. 253535, female "u" 2.55 mm, and 7 other specimens.

Relationship.—Differing from *N. brocha* in the lobate article 2 of pereopod 7, the presence of only 1 spine on the inner ramus of uropod 3, the presence of only one (but giant) raker on the left mandible, the absence of raker on the right mandible, the shorter main spine on the telson, and the lack of marginal spines on the outer rami of uropods 1–2.

Distribution.—Belize, Carrie Bow Key, 29 m.

Netamelita barnardi McKinney, Kalke, & Holland, 1978

Netamelita barnardi McKinney, Kalke, & Holland, 1978:136, figs. 1–2.

The following composition is parallel to that of the other species described above but is taken solely from the original description; one undescribed character is marked with a ?.

Diagnosis.—Coxa 1 moderately curved forward. Article 2 of pereopods 5–6 not

lobed, of 7 lobed posteroventrally, of 5–7 weakly serrate. Epimera 1–3 with small sharp posteroventral tooth, epimeron 1 lacking thick anteroventral spine, epimeron 2 with numerous ventral setae, epimeron 3 with 5 long ventral spines. Outer rami of uropods 1 and 2 not significantly shortened, with marginal spine(s). Peduncle of uropod 2 without huge spine. Main apical spine of telson about one-fourth as long as telson.

Subsidiary observations.—Article 1 of mandibular palp short, with one seta, article 2 naked, article 3 with 3 apical setae. Left mandible with one raker, right with ?. Outer plate of maxilla 1 with 9 spines, apex of palp article 2 with 8 elements. Outer plate of maxilliped with 2 long apical comb-setae, and singles or pairs of medial and medioventral shorter simple spines, palp article 3 expanded, lobate apicolaterally. Peduncle of uropod 1 with apical displaced spines, lateral one of medium size, medial one of large size, each apex also with small partner spine. Peduncle of uropod 2 with pair of apico-dorsolateral spines, with quartet of apicomedial spines, plus 2 sets of more proximal medial spine(s) in tandem. Outer and inner rami of uropod 1 with 4 and 3 apical spines and one marginal spine; of uropod 2 each ramus with 5 apical spines and 2 marginal spines; inner ramus of uropod 3 with 2 spines. Apex of each telsonic lobe with one short spine, one apicolateral penicillate setule and pair of lateral penicillate setules near apex but more remotely than in other species described herein.

Distribution.—Western Gulf of Mexico, 15–40 m.

Acknowledgments

Fieldwork for this report was supported by Smithsonian's CCRE committee under CCRE Contribution No 312; we thank Dr. Klaus Rutzler, head of this program, and Mike Carpenter, for their assistance. The first author was supported by NSF Grants BSR 8515186 and BSR 89156688. Linda Lutz of Vicksburg, Mississippi, inked our drawings.

Literature Cited

Barnard, J. L. 1962. Benthic marine Amphipoda of southern California: Families Tironidae to Gammaridae.—Pacific Naturalist 3:73–115.

———, & C. M. Barnard. 1983. Freshwater Amphipoda of the world. Hayfield Associates, Mt. Vernon, Virginia, 2 volumes.

McKinney, L. D., R. D. Kalke, & J. S. Holland. 1978. New species of amphipods from the western Gulf of Mexico.—Contributions in Marine Science 21:133–159.

Vonk, R. 1988. *Psammomelita uncinata* n. g., n. sp. (Crustacea, Amphipoda, Melitidae) from infralittoral sand interstices on Curacao.—Stygologia 4:166–176.

(JDT) Reef Foundation, Box 569, Big Pine Key, Florida 33043; (JLB) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 593–602

SKUPHONURA KENSLEYI (CRUSTACEA: ISOPODA), A NEW ANTHURIDEAN SPECIES FROM THE CARIBBEAN COAST OF COLOMBIA

Richard C. Brusca and Hans-Georg Müller

Abstract.—A new species of Anthuridea, *Skuphonura kensleyi,* is described from the Caribbean coast of Colombia, where it inhabits littoral and shallow-water habitats. The new species resembles *S. lindae* Menzies & Kruczynski, 1983 and *S. itapuca* Kensley, 1980, but is distinguished by a suite of distinct features. The genus *Skuphonura,* which is restricted to the New World, is rediagnosed, and a key to the known species of *Skuphonura* is presented.

Barnard (1925) created the genus *Skuphonura* for the new species, *S. laticeps,* based on three male specimens collected near St. Thomas, U.S. Virgin Island, and one female from Tobago. The genus received scant attention until Kensley (1980) redescribed *S. laticeps* based on the syntypes (tentatively excluding the one female specimen) and described two additional species from South America, *S. itapuca* (from Rio de Janeiro, Brazil) and *S. ecuadorensis* (from La Libertad, Ecuador). Kensley (1980) also presented a revised diagnosis for the genus, noting its similarity to *Mesanthura.* He suggested that two features immediately separating these two genera are the presence of a persistent pigment pattern in *Mesanthura* (thought to be absent in *Skuphonura*), and the [presumed always] uniarticulate flagella of both the antennules and the antennae of *Skuphonura* (the antennular and antennal flagella of *Mesanthura* both comprise more than one article). In 1983, Menzies & Kruczynski described a fourth species of *Skuphonura, S. lindae* from central west Florida. We herein describe a fifth species, *Skuphonura kensleyi,* from the Caribbean coast of Colombia, and provide a new diagnosis and comments on the genus and a key to the five known species.

Because the genus and its species are poorly known, the species description is rather detailed and repeats some characters currently regarded as generic attributes. All specimens are deposited in the National Museum of Natural History, Smithsonian Institute (USNM).

Systematics

Subphylum Crustacea Pennant
Class Malacostraca Latreille
Superorder Peracarida Calman
Order Isopoda Latreille
Suborder Anthuridea Leach
Family Anthuridae Leach
Skuphonura Barnard, 1925

Skuphonura.—Barnard, 1925:145, text fig. 10, pl. 4, fig. 15—Miller, 1968:26 (fig. 4); Kensley, 1980:731 (figs 5–9); Menzies & Kruszynski, 1983:30 (fig. 10); Kensley & Schotte, 1989:58 (fig. 25).

Diagnosis.—Cephalon with posteromedial, toothlike, ventral cephalic process situated behind the mouthparts and directed anteriorly; males with one ventral cephalic process, females often (always ?) with two processes. Cephalon and body with or without pigment pattern; cephalon may be markedly wider anteriorly due to rounded, expanded, anterolateral lobes that bear the eyes (in 2 of the 5 known species). Antennules 4- to 6-articulate, females of a given

species possibly possessing one more article than males; antennae 6- to 8-articulate; mandible with 3-articulate palp, distal article markedly shorter than articles 1 and 2; with well-developed incisor and lamina dentata, and lobe-like molar process; maxilliped 5-articulate, terminal article very small and often somewhat immersed in penultimate article, penultimate article largest, antepenultimate article shorter than adjacent articles. Fused coxal plates usually visible in dorsal aspect on pereonites 2–7; pereopod 1 subchelate, with large propodus, acutely triangular carpus, and very short merus; posterior pereopods with acute scales on margins of propodi and dactyli; pereopods 1–7 carpi triangular. Pleonites fused, but with suture lines (incisions) present ventrolaterally; fusion of pleonite 6 with pleonite 5 and with telson demarcated dorsally by deep grooves; pleotelson ovate, distally rounded, with pair of basal statocysts; pleopod 1 exopod operculate, somewhat indurate; appendix masculinae arise about ⅓ way up margin of pleopod 2 endopods and extended beyond endopod apecies; uropodal exopod ovate, with distal notch.

Remarks.—There has been some confusion regarding the number of articles in the peduncle and flagellum of the antennules and antennae in this genus. Further confusion arises from the fact that females (in any given species) may possess an antennule with one more article than found in males, this being the short fourth article which we regard as the first flagellar article. Thus the antennules of *S. itapuca* and *S. ecuadorensis* appear to have 3 peduncular articles and one flagellar article in males, but 3 pedunuclar articles and 2 flagellar articles in females. In *S. linae,* females seem to have 3 peduncular articles and 3 flagellar articles (according to Menzies & Kruczynski 1983). However, the literature is rather unclear on this issue, as the distalmost flagellar articles are often compressed and difficult to see. Males are not yet known for *S. lindae,* and females are not yet known for *S. laticeps* and *S. kensleyi.*

The genus *Skuphonura* does not appear to possess any unique defining synapomorphies. It is very similar to four other genera of Anthuridae: *Mesanthura* Bernard, 1914; *Apanthura* Stebbing, 1900; *Apanthuretta* Wägele, 1981; and *Apanthuropsis* Poore & Lew Ton, 1985. One of the most diagnostic features of *Skuphonura* is the ventral cephalic process (a large antero-ventrally directed process that arises just posterior to the maxillipeds). In those species where both sexes have been described (*S. itapuca* and *S. ecuadorensis*), males have one process and females have two processes (one behind the other). However, certain species of *Apanthura* and *Apanthuretta* also possess a ventral cephalic process (e.g., *Apanthura thryptomene* Poore & Lew Ton, 1985; *Apanthura xanthorrhoea* Poore & Lew Ton, 1985; *Apanthuretta correa* Poore & Lew Ton, 1985). The maxillipeds, pereopods, and uropods are also very similar among *Skuphonura, Apanthura, Apanthuretta,* and *Apanthuropsis.* The segmentation of the antennules and antennae, and presence vs. absence of body pigmentation, cannot be relied upon to discriminate *Skuphonura* from *Mesanthura.* However, it does appear that pigmented *Mesanthura* specimens retain their pigmentation for many years in alcohol preservative, perhaps longer than do pigmented specimens of *Skuphonura* (as noted by Kensley 1980).

Skuphonura kensleyi, new species
(Figs. 1–5)

Material examined.—Holotype, immature: Colombia, Santa Marta, Punta de Betin, under algal-covered rocks on sandy bottom, 2–3 m depth, 24 Dec 1985 (USNM 250983). Paratypes: 1 male, 1 immature, 2 postmancas, and 4 mancas, taken with the holotype; 1 male and 1 postmanca, same locality, in coral rubble, 6 m depth, 4 Aug 1985; 2 immatures, same locality, under rocks on sand bottom, 0–1 m depth, 28 Jan 1989; 3 males, same locality, under rocks

on sandy bottom with debris, 1–2 m depth, 4 Feb 1989.

Description.—Immature stage: Length (front of cephalon to apex of pleotelson) 3.0–5.7 mm; relative lengths of body segments C < 1 > 2 > 3 < 4 = 5 > 6 > 7. Cephalon and pereon with distinct pigment reticulations (as figured). Cephalon widest at midline, lateral margins slightly convex; eyes small, with 5–6 ommatidia, well-pigmented. Fused coxal plates of all pereonites visible in dorsal aspect. Pleonites 1–6 fused; segments 1–5 indicated laterally by short incisions; pleomere 6 with posterior marginal notch; with many setae on distal third of pleotelson, arranged in characteristic pattern.

Antennule articles decreasing in size distally; second article with 5, and third with 2, stiff, laterally directed simple setae near outer distal margin; flagellum 3-articulate, second article longest, third article with 2 simple setae and a distal aesthetasc. Antenna second article longest, flared and grooved to accommodate peduncle of antennule; flagellum 1-articulate, with numerous simple apical setae. Mandible with 3-articulate palp; second article with 2 simple setae and short distal article with 3 simple setae; incisor of single cusp, lamina dentata with about 6 serrations, molar process oval and simple. Maxilla slender, with 6 distal teeth and 1 small seta between the distal and penultimate tooth. Maxilliped with elongate-oval endite bearing an apical seta; second segment of 3-articulate palp largest; distal article smallest and with about 6 medially-directed robust setae.

Pereopod 1 subchelate, propodus with simple setae. Pereopods 2–7 propodi inferior margin with several setae and a robust distal spine; pereopods 5–6 propodi with marginal scales; pereopod 7 propodus with 2 serrate apical spines. Pereopods 1–7 dactyli with distal setae; dactylus of pereopod 7 additionally with marginal scales on inferior and superior margins. All pereopods with carpus triangular; carpus of P-1 with toothlike projection at posterodistal corner; P-4 to P-7 with a short stout spine at posterodistal corner of carpus.

Uropodal endopod extending somewhat beyond apex of pleotelson; exopod oval, with shallow apical notch; endopod shorter than protopod, 1.9 times longer than wide.

Male: Length 4.5–5.7 mm. Similar to immature stage; with distinct ventral cephalic process; eyes somewhat larger than in immatures; antennule flagellum with 3 compressed articles, two distal ones bearing many aesthetascs; palm of pereopod 1 propodus excavate, with rounded proximal and distal tubercles; in one of the smallest males observed, the distal tubercle is reduced; medial surface of propodus with several setae; pereopod 7 more slender than other pereopods; inferior margin of propodus and distal inferior margin of dactylus with row of rounded scales. Exopod of pleopod 1 operculiform, distal margin with about 28 plumose marginal setae (setules not illustrated); appendix masculinae of pleopod 2 endopod articulating about ⅓ distance from base; exopod somewhat shorter and wider than endopod; endopod with about 6, exopod with about 8 distal plumose marginal setae (setules not illustrated).

Female: Unknown.

Postmanca: Length 1.8–2.6 mm. Similar to immature stage; pigment reticulations on pereonites and pleon indistinct; pleotelson similar to immatures with distinct setation; shape of pereopods as in immatures, although all segments less setose.

Manca: Length 1.7–2.1 mm. Similar to postmanca except all segments of pereopods generally less setose, and pereopod 7 wanting.

Remarks.—Skuphonura kensleyi is somewhat similar in appearance to *S. lindae* Menzies & Kruczynski, 1983 and *S. itapuca* Kensley, 1980. Of the known species in this genus, these three lack the greatly expanded anterolateral cephalic lobes. Although Kensley (1980) stated that in *S. itapuca* the cephalon is anteriorly slightly wider than posteriorly, examination of the type series revealed that the lateral margins of the

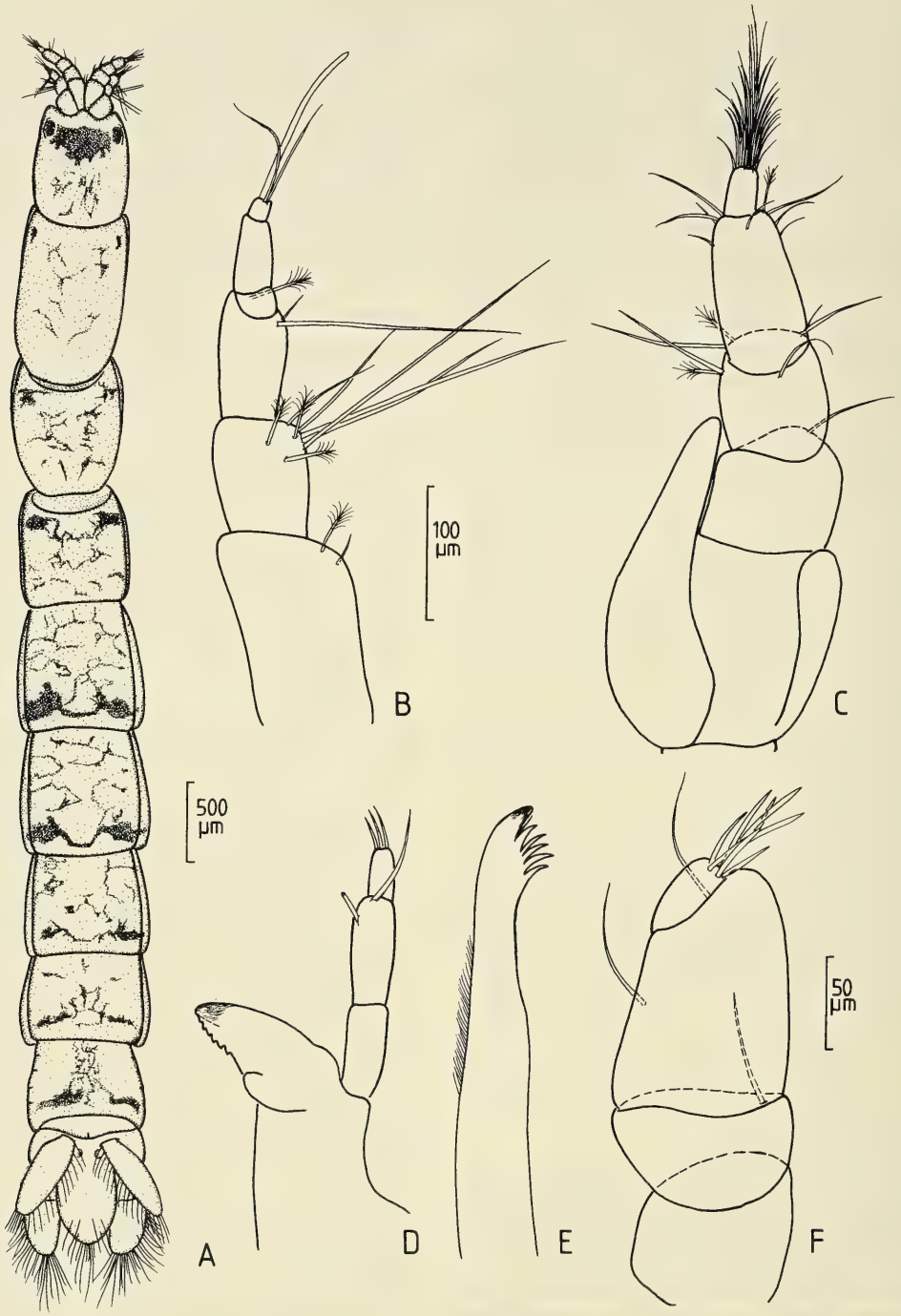


Fig. 1. *Skuphonura kensleyi* n. sp., holotype. A, dorsal view. B, antennule. C, antenna. D, mandible. E, maxilla. F, maxilliped.

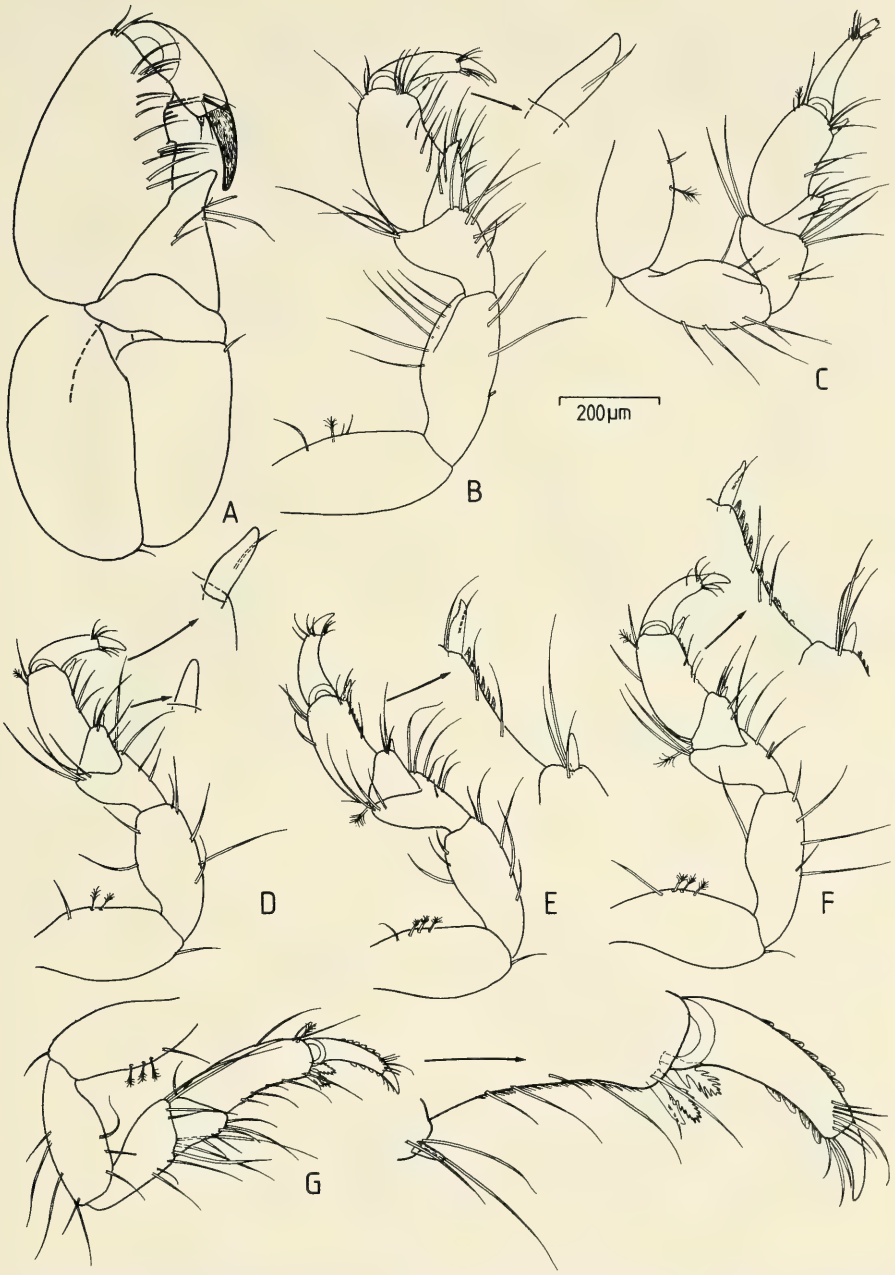


Fig. 2. *Skuphonura kensleyi,* n. sp., holotype. A, pereopod 1. B, pereopod 2. C, pereopod 3. D, pereopod 4. E, pereopod 5. F, pereopod 6. G, pereopod 7.

cephalon are evenly convex, with the widest region being slightly anterior to the middle of the cephalon; large anterolateral lobes are lacking.

Skuphonura kensleyi is a shallow-water species found from the intertidal zone to a depth of 6 m. It has been found in association with coral rubble and rocks on sandy

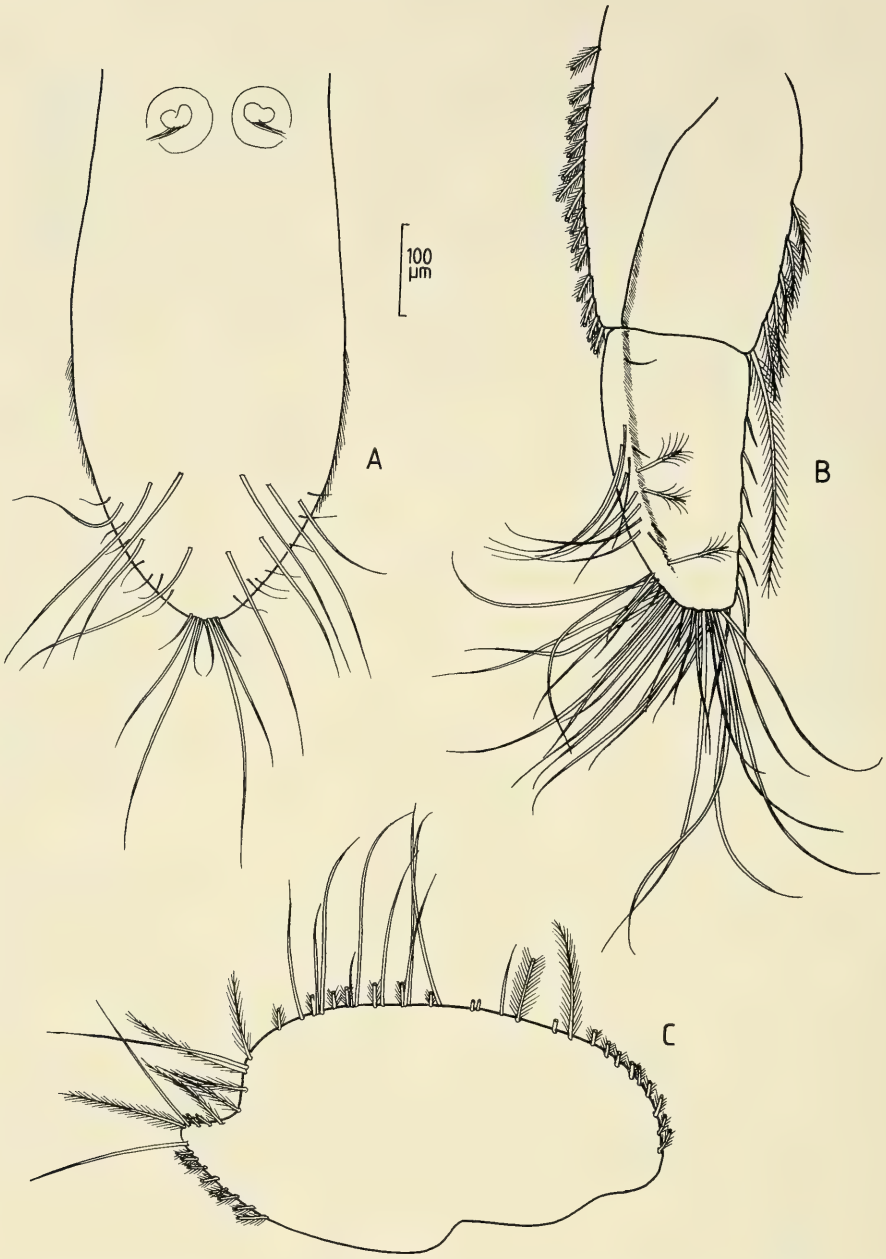


Fig. 3. *Skuphonura kensleyi,* n. sp., holotype. A, telsonic region of pleotelson. B, uropodal peduncle and endopod. C, uropodal exopod.

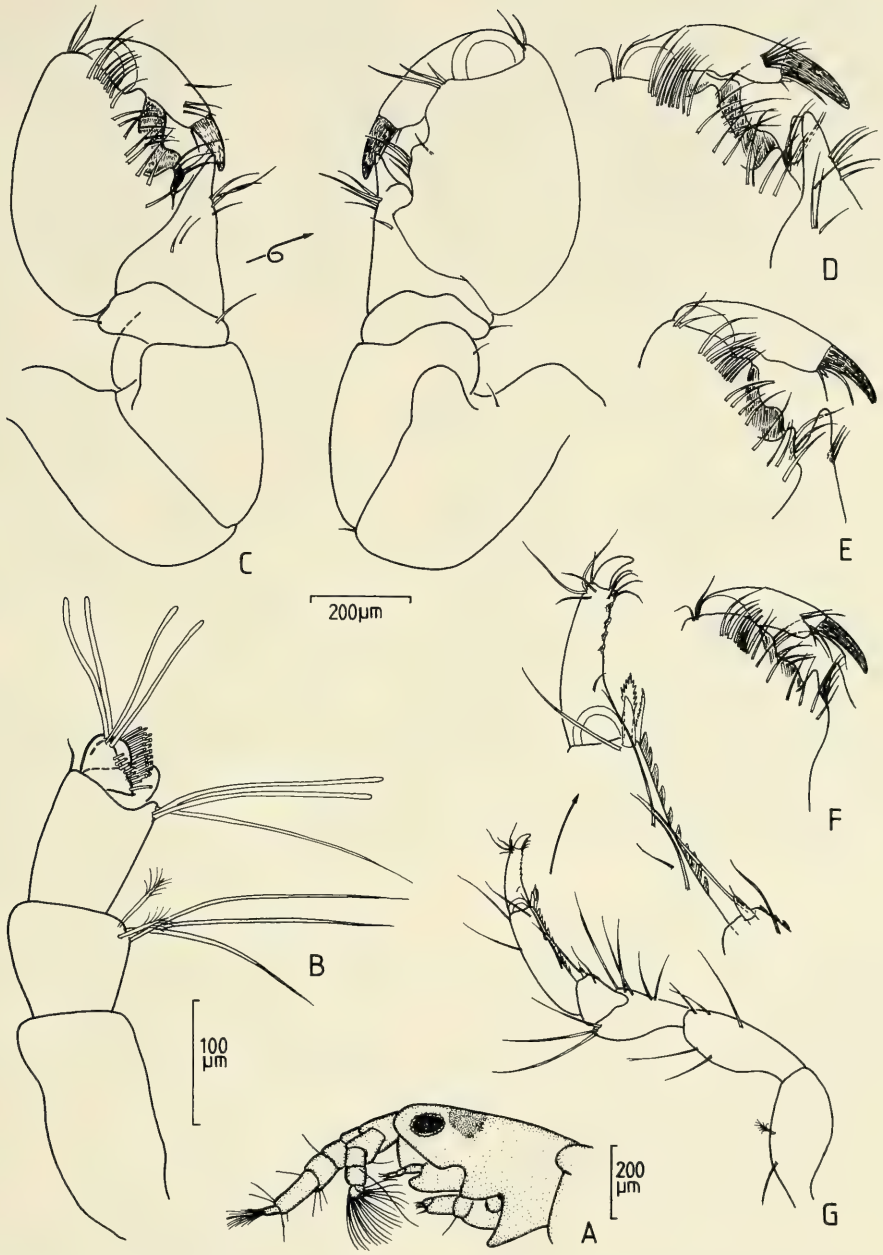


Fig. 4. *Skuphonura kensleyi,* n. sp., male paratypes. A, cephalon, lateral view. B, antennule. C, pereopod 1 inner and outer surfaces. D–F, distal portion of pereopod 1 from three different specimens. G, pereopod 6.

bottoms. Surprisingly, this new species has been found exclusively at Punta de Betin in Santa Marta, although extensive collecting was carried out over approximately 70 km of coastline in this region for more than one year.

Etymology.—We take great pleasure in naming this species after Dr. Brian Kensley,

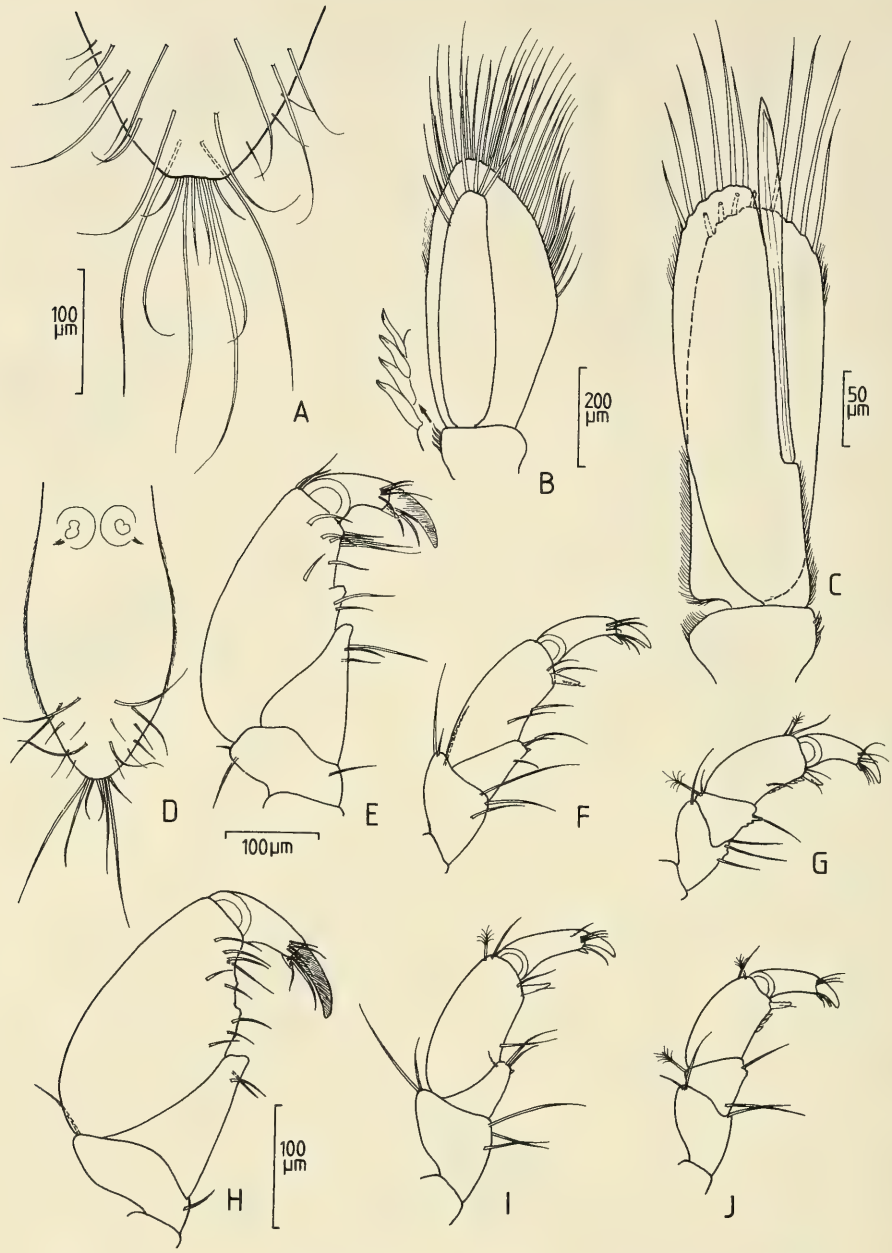


Fig. 5. *Skuphonura kensleyi,* n. sp., paratypes. A, distal region of pleotelson (male paratype). B, pleopod 1 (male paratype). C, pleopod 2 (male paratype). D, telsonic region of pleotelson (postmanca). E, distal region of pereopod 1 (postmanca). F, distal region of pereopod 2 (postmanca). G, distal region of pereopod 4 (postmanca). H, distal region of pereopod 1 (manca). I, distal region of pereopod 2 (manca). J, distal region of pereopod 4 (manca).

whose work has contributed greatly to our understanding of the genus *Skuphonura* and anthurideans in general.

Key to the Species of *Skuphonura*

1. Cephalon markedly wider anteriorly than posteriorly, with large rounded anterolateral lobes bearing the eyes 2
– Cephalon not markedly wider anteriorly than posteriorly, without large rounded anterolateral lobes . 3
2. Pleonite 1 with large, anteriorly-directed, ventral projection; pereopod 1 propodus without tubercles on inferior margin, but with a low, rounded, convexity; uropodal endopods barely reach pleotelson apex ..... *S. laticeps*
– Pleonite 1 without a large ventral projection; pereopod 1 propodus with 2–3 distinct tubercles on the inferior margin; uropodal endopods extended barely beyond pleotelson apex ..... *S. ecuadorensis*
3. Uropodal endopods extended barely beyond pleotelson apex; pereopod 1 propodus with a broad flat lobe on inferior margin .....*S. lindae**
– Uropodal endopods extended well beyond pleotelson apex; pereopod 1 not as above, instead with propodus with 1–3 large tubercles on inferior margin 4
4. Dactyli of pereopods 4–7 with triangular, marginal, spinose scales; pereopod 2 unguis length = 20% length of dactylus; pereopod 1 propodus with 2–3 tubercles on inferior margin; mandibular molar bilobed ..... *S. itapuca*
– Dactylus of pereopod 7 only with triangular, marginal, spinose scales; pereopod 2 unguis length = 35–40% length of dactylus; pereopod 1 propodus with 1–2 tubercles on inferior margin; mandibular molar single-lobed ..... *S. kensleyi,* n. sp.

*Note: *Skuphonura lindae* may not belong to this genus. Generic characters of *Skuphonura* that may be lacking in *S. lindae* include: pleopod 1 exopod indurate and operculiform; cephalon with midventral toothlike process; carpi of pereopods 4–7 distinctly triangular; pleotelson with a pair of statocysts. However, until type material of *S. lindae* can be examined the question remains open.

Acknowledgments

Field work in Colombia by H.-G.M. was supported by a grant from the German Academic Exchange. The Instituto de Investigaciones Marinas de Punta de Betin (INVEMAR/COLCIENIAS) in Santa Marta provided technical help with field work. Work on this project also was funded in part by grants to R.C.B. from the U.S. National Science Foundation, The Weiler Foundation, and The National Geographic Society.

Literature Cited

Barnard, K. H. 1925. A revision of the family Anthuridae (Crustacea Isopoda), with remarks on certain morphological peculiarities.—Journal Linnaean Society (Zoology) 36:109–160.

Kensley, B. 1980. Records of anthurids from Florida, Central America, and South America (Crustacea: Isopoda: Anthuridae).—Proceedings Biological Society of Washington 93:725–742.

———, & M. Schotte. 1989. Guide to the marine isopod crustaceans of the Caribbean.—Smithsonian Institution Press, Washington, D.C., 308 pp.

Menzies, R. J., & W. L. Kruczynski. 1983. Isopod Crustacea (Exclusive of Epicaridea).—Memoirs of the Hourglass Cruises, Florida Department of Natural Resources, St. Petersburg, Florida 126 pp.

Miller, M. A. 1968. Isopoda and Tanaidacea from buoys in coastal waters of the continental United States, Hawaii, and the Bahamas (Crusta-

cea).—Proceedings of the United States National Museum 125(3652):1–53.

Poore, G. C. B., & H. Lew Ton. 1985. *Apanthura, Apanthuretta,* and *Apanthuropsis* gen. nov. (Crustacea: Isopoda: Anthuridae) from southeastern Australia.—Memoirs Museum of Victoria 46:103–151.

(RCB) San Diego Natural History Museum, San Diego, California, 92112; (HG-M) Zoologisches Institut, Neues Tierhaus, Heinrich-Buff-Ring 29, D-6300 Giessen, Germany.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 603–612

PARANEBALIA BELIZENSIS, A NEW SPECIES FROM SHALLOW WATERS OFF BELIZE, CENTRAL AMERICA (CRUSTACEA: MALACOSTRACA: LEPTOSTRACA)

Richard F. Modlin

Abstract.—*Paranebalia belizensis,* a new species of leptostracan from *Halimeda* habitats in the shallow waters surrounding Twin Cays, a mangrove archipelago in Belize, Central America, is described using the Dahl Model. Subtle, but consistant, differences separate *P. belizensis* from the ubiquitous *P. longipes.*

In shallow coastal waters of the western Atlantic Ocean and Caribbean Sea leptostracans of the genus *Paranebalia* are represented by a single known species, *P. longipes* Willemoes-Suhm (1875). This species has been reported from shallow waters off Bermuda (Willemoes-Suhm 1875, Sars 1887, Verrill 1923, Clark 1932), Virgin Islands (Thiele 1904), Bahamas and Southern Florida (Brattegard 1970). This paper uses Dahl's (1985) taxonomic model to describe a new species of *Paranebalia* from waters off Belize, Central America, in the western Caribbean Sea.

Specimens were obtained from a variety of locations in the Twin Cays archipelago. Masses of *Halimeda* growing on submerged parts of proproots of the red mangrove, *Rhizophora mangle,* were hand-collected and bagged. The algal masses were washed, piece by piece, in a bucket of seawater of ambient salinity and temperature. The residue remaining after the bucket water was filtered through a 0.2 mm mesh net bag was fixed in 7–10% Formalin, stained with Phloxine-B to facilitate sorting and transported to my Huntsville, Alabama laboratory. After sorting specimens were preserved in 70% ethanol.

A variety of measurements were made on specimens and their defining structures using an ocular reticle calibrated by a stage micrometer. Total length is the distance along the dorsal midline from the articulation of the rostrum to the posterior margin of the telson. Carapace length is the distance along the dorsal midline from the articulation of the rostrum to the margin of the posterodorsal cleft. Rostral length is measured along midline; width is measured across widest part of proximal half. Unless otherwise specified measurements on other structures are defined as follows: length is the longest linear distance between the ends of the structure and width the widest linear distance from side to side.

All statistical analyses were made using the ABSTAT Statistical Software package.

Paranebalia belizensis, new species
Figs. 1–5

Type material.—Twin Cays, Belize, Central American R. F. Modlin, 14 Jul 1989, Sample number 071489M31; Holotype 1 female, 3.3 mm total length (USNM 250527); Allotype 4 males, 1.7–2.1 mm (USNM 250528); Paratype 14 females, 1.4–3.6 mm and 3 ovigerous, 2.9–3.6 mm (USNM 250529).

Material examined.—Collected by R. F. Modlin at Twin Cays, Belize, Central America (16°04′N, 88°50′W). Sample numbers are composed, respectively, of month, day, year and station number, followed by the number of male-female-ovigerous-juvenile specimens examined: 1211588M31, 0-27-1-0; 121588M34, 2-70-0-8; 121788M30, 0-3-0-0; 121788M31, 0-5-1-0; 121788M34,

11-126-9-78; 070689M31, 12-109-6-57; 070689M34, 6-59-0-28; 071489M31, 15-76-3-11; 071489M35, 7-60-2-57.

Female.—Body robust, transparent, colored beige in living or preserved specimens, but eggs and ripe gonadal tissue color gravid females red. Carapace antero- (Fig. 1A) and posterolateral margins rounded without specialized spines, surface without any texture, posterodorsal cleft deep exposing all abdominal segments, anterodorsal margin articulating with rostrum, mean carapace length/total length ratio = 0.488 (standard error of mean = *SE* = 0.013, sample size = *n* = 52, range of carapace lengths (mm) measured = R = 0.6–1.75).

Rostrum (Fig. 1B) ovoid, broadly rounded in cross-section, apex with 1–2 subterminal spines, 2 obvious muscle scars near posterior margin, without sculpturing on dorsal or ventral surfaces, mean width/length ratio = 0.516 (*SE* = 0.013, *n* = 22).

Dentation of posterodorsal margin of pleonites 6 and 7 composed of triangular, sharply pointed denticles of equal length, denticle length = ca. 20 μm (Fig. 2).

Eyestalk (Fig. 1C) cylindrical, elongate, distal corneal region heavily armed with many robust spines, outer margin of proximal half with 5–7 small sharp spines; cornea oval, averages 49% of eyestalk length (*SE* = 3.0, *n* = 17).

Antennule peduncle (Fig. 1D) of 4 articles. Article 1 (not illustrated) small and inconspicuous; article 2 length/width ratio about 3.0, average length = 0.33 mm (*SE* = 0.03, *n* = 15), with distal clump of setae composed of about 12 short fine and 2 long thick setae; article 3 slightly shorter than article 2, average length 0.29 mm (*SE* = 0.03, *n* = 15), with 2 clumps of fine setae on distal half of lateral margin, 3 small setae on medial margin distally; article 4 short, average length 0.11 mm (*SE* = 0.02, *n* = 15), with lateral flange containing 7–10 robust denticles, inner edge of denticles with minute serrations. Antennule flagellum composed of 6 articles, proximal article about 6.7 times longer than others, 4 filiform esthetascs, 2 sets of paired pectinate setae and simple seta distolaterally, 3 simple setae dorsally; article 2 with filiform esthetasc, distolateral set of paired pectinate setae and simple seta, single simple seta dorsally; articles 3 to 6 each with set of paired pectinate setae and simple seta in distal lateral corner, and single simple seta dorsally; article 6 with 3 additional long naked terminal setae. Antennule scale blade-like, length/width ratio about 2.3, setose only on lateral and distal margins.

Antenna peduncle (Fig. 1E) composed of 3 articles, average length = 0.88 mm (*SE* = 0.07, *n* = 13). Article 1 short, inconspicuous; article 2 rectangular, length/width ratio about 2.4, average length = 0.31 mm (*SE* = 0.03, *n* = 13); article 3 longest, average length = 0.45 mm (*SE* = 0.03, *n* = 15), with 3 clumps of fine setae and 2 short robust spines on lateral margin, one long plumose seta at midlength of medial margin, and 4 plumose setae and minute spine on distomedial corner. Antennal flagellum of 5 articles, 0.65 times as long as peduncle, average length 0.58 mm (*SE* = 0.05, *n* = 15); proximal article average length = 0.23 mm (*SE* = 0.03, *n* = 15), 0.66 times longer than combined length of articles 2–5, fine setae arising from each articulation.

Mandibular palp (Fig. 3A) composed of 3 articles. Article 1 small, inconspicuous; article 2 curved, 1.1 times as long as article 3, with single long subterminal seta; article 3 margins nearly parallel tapering terminally, single terminal seta sharply curved medially, 2 rows of uniformly arranged robust setae along medial margin setae of both rows increasing in length distally, long pinnate inner row of setae originates in proximal ⅓, short naked outer row of setae originates in distal ⅓, 1 long straight terminally directed submarginal seta originates at midlength on each side of marginal rows of setae.

Maxillule (Fig. 3B) sympod with 2 endites; endite 1 flat, expanded, margin curved

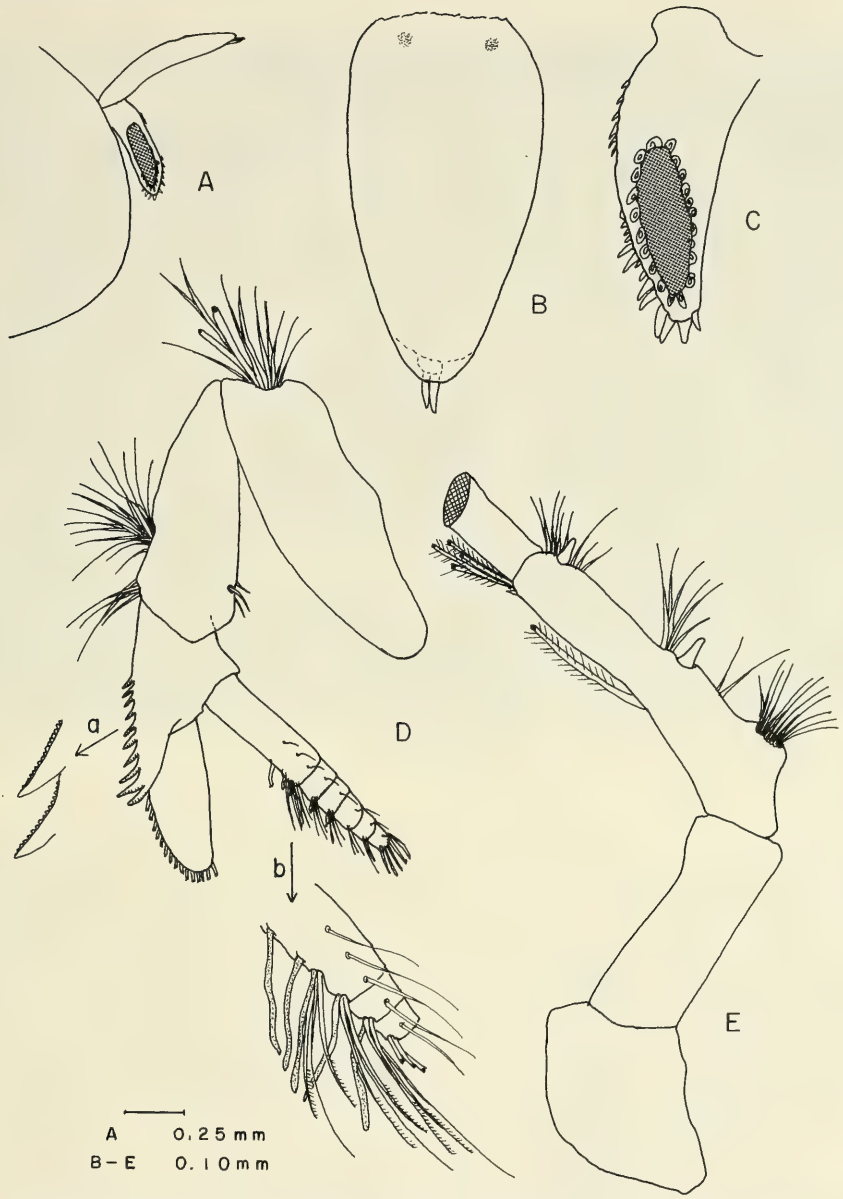


Fig. 1. *Paranebalia belizensis,* new species: A, Anterior profile; B, Rostrum; C, Eye stalk; D, Antennule, a. serration on denticles of flange, b. setation on proximal 3 articles of flagellum; E, Antennal peduncle. Female, 3.3 mm.

with 10 long plumose setae and many minute hair-like setae; endite 2, pedestal-like with single subterminal plumose seta, articulates with short terminal segment with truncated distal margin containing row of robust spines. Palp composed of 3 articles; articles 1 and 2 short; article 3 very long, sharply flexed in proximal ⅙, inner margin with 13–14 long naked setae.

Maxilla (Fig. 3C) with 4 endites; endite 1, expanded, distal margin curved with long thin plumose setae; endites 2 and 3, rect-

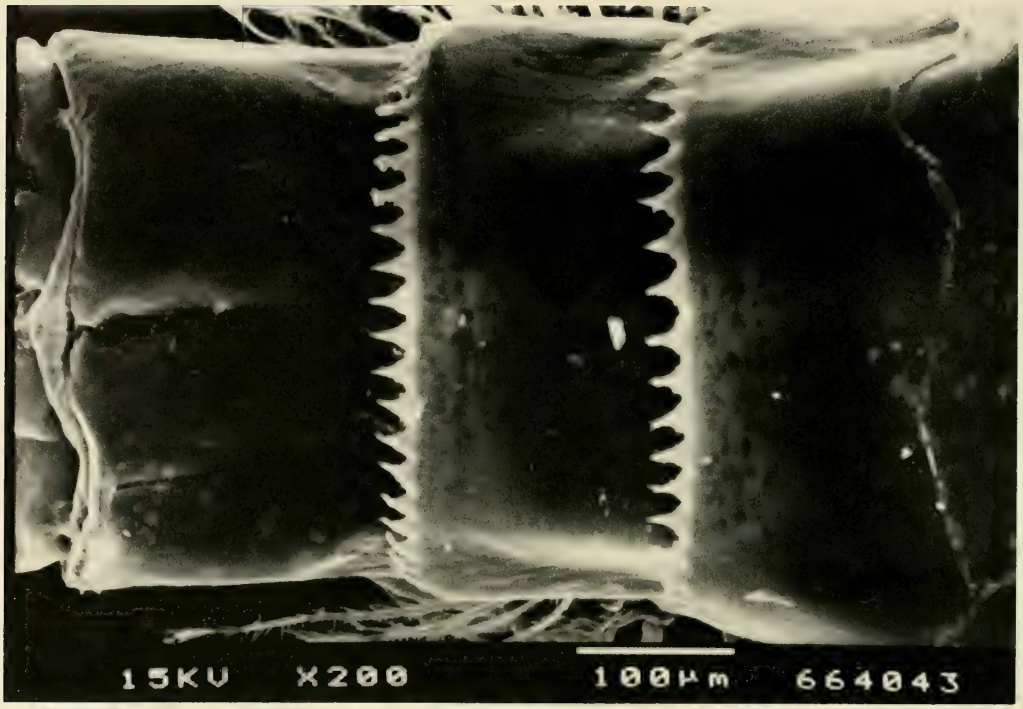


Fig. 2. *Paranebalia belizensis,* new species. Scanning electron micrograpy of dentition on the posterodistal margin of pleonites 6 and 7, and posterodistal margin of the telson. Female, 3.5 mm.

angular, distal margin truncate with long thin plumose setae; endite 4, short, rounded, distal margin with 2 long thick plumose setae and 1 long subterminal naked seta; endopod blade-like, composed of 2 articles, proximal about 0.5 times as long as distal, distal article with 3 long thick terminal plumose setae; exopod blade-like, outer and distal margins with 10 long, stout plumose setae.

Shape and size of thoracopods vary with life stage, but shape is characteristic of the genus. Figures 3D to F outline thoracopods 1, 4 and 8 from a mature non-gravid female. Sympods phyllopodous, medial margin setose with paired thin pinnate setae; epipods small, narrow, setose with many short naked setae along lateral margin; exopod of thoracopods 1 and 8 about ½ as long as endopod, exopod of thoracopods 2 to 7 about 0.8 times as long as endopods, all narrow, tapering distally, lateral margin setose with stiff pennate setae; endopods narrow, tapering distally, medial margin and distal half of lateral margin heavily setose with paired thin pinnate setae. Marginal setation is the same on all thoracopods. However, it is of little taxonomic value, since these setae exhibit drastic transformations during the female sexual cycle (Dahl 1985).

Pleopod 1 (Fig. 4A) peduncle dorsal surface with submarginal serration composed of 7–8 denticles laterally; exopod 0.68 times as long as endopod (SE = 0.02, n = 15), lateral margin with compact row of spines increasing in length distally terminating with single robust spine with minute subterminal flagellum, distal margin with 1 long flexed and 2 shorter subequal spines each with minute subterminal flagellum, 3 subterminal setae distally; endopod 0.94 times as long as peduncle (SE = 0.3, n = 15), with

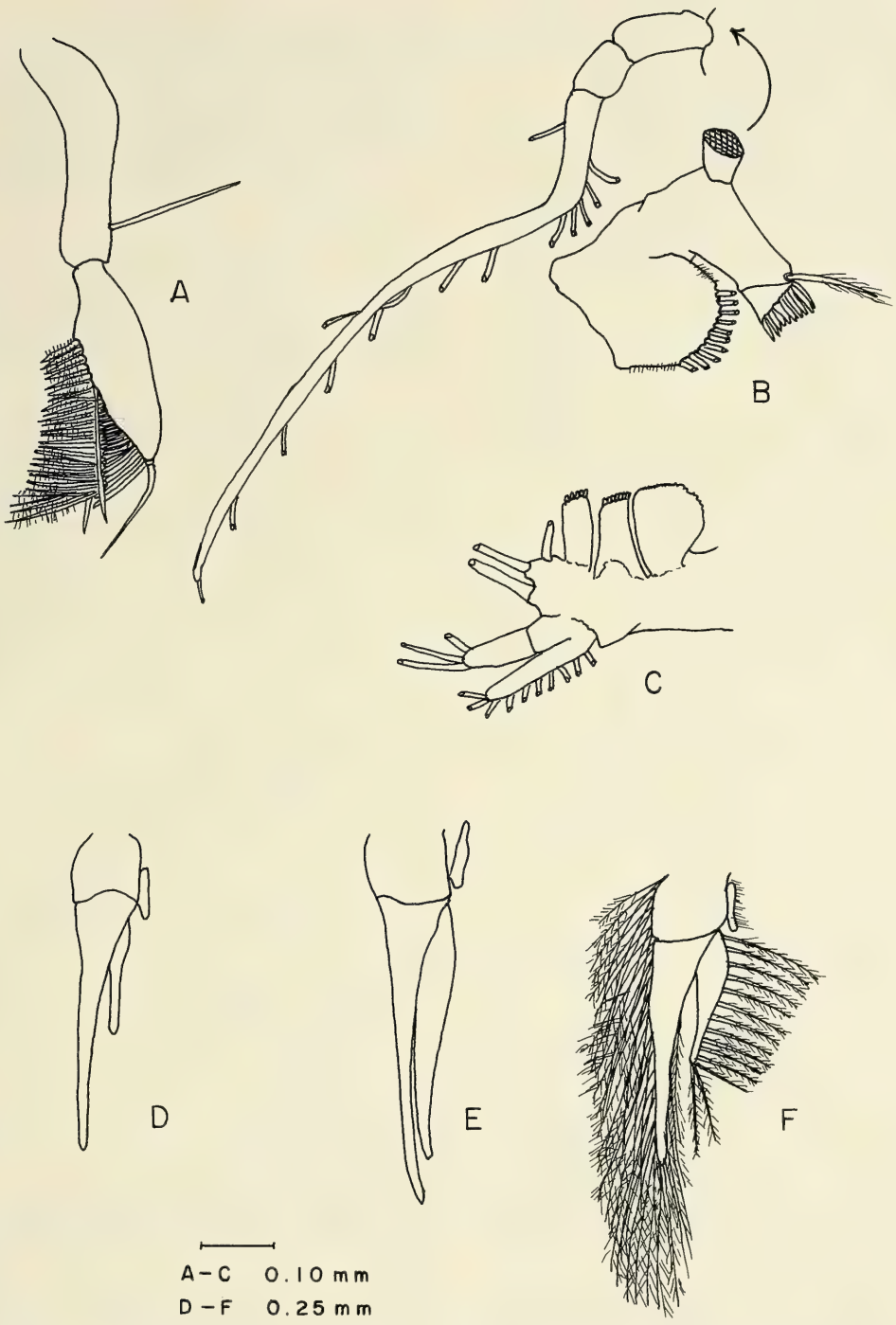


Fig. 3. *Paranebalia belizensis,* new species: A, Distal 2 articles of mandibular palp; B, Maxillule; C, Maxilla; D, Thoracopod 1 (marginal setation omitted); E, Thoracopod (marginal setation omitted) 4; F, Thoracopod 8. Female, 3.3 mm.

proximomedial retinaculum, lateral margin setose, distal margin with 2 short spines each with minute subterminal flagellum.

Pleopods 2, 3 and 4 similar, peduncle of each similar to pleopod 1. Pleopod 2, exopod 0.84 times as long as endopod (SE = 0.01, n = 12); endopod 0.93 times as long as peduncle (SE = 0.02, n = 12). Pleopod 3, exopod 0.94 times as long as endopod (SE = 0.04, n = 14); endopod 0.91 times as long as peduncle (SE = 0.05, n = 14). Pleopod 4 (Fig. 4B), exopod 0.99 times as long as endopod (SE = 0.05, n = 14), lateral margin with 6 pair of robust flagellated spines, distal 5 pair with adjacent single pinnate seta, robust terminal flagellated spine about twice as long as adjacent marginal spine; endopod 0.92 times as long as peduncle (SE = 0.04, n = 14), lateral margin setose, 2 terminal flagellated spines.

Pleopods 5 and 6 uniramous. Pleopod 5 (Fig. 4C), lateral margin with about 8 short flexed setae, distal margin with 3 robust flagellated spines and 6 short flexed setae, 3 short pinnate submarginal setae. Pleopod 6 (Fig. 4D), lateral margin distal half with 1 flexed seta, 3 pinnate setae and 1 thin spine with long subterminal flagellum, medial margin distal half with short robust spine and 2 flexed setae, distal margin with 2 robust spines each with minute subterminal flagellum, 1 thin spine with long subterminal flagellum, 1 thin spine with bulbous tip, and 2 flexed setae.

Pleonite 8 (Fig. 2) posterodorsal margin with medial symmetrical bulge.

Caudal ramus (Fig. 4E) 0.52 times as long as carapace (SE = 0.02, n = 12), lateral and medial margins setose with short flexed setae, distal end of medial margin serrated with small clump of minute setae at origin of serration, terminally 1 long flexed seta and 1 long thin naked seta submarginally.

Description male.—Smaller than female (mean total length = 1.96 mm, SE = 0.04, range = 1.5–2.4, n = 50), but structurally similar to female except for flagellum of antennule (Fig. 5A, B). Antennule flagellum greatly inflated, articulations between individual segments visible only near terminal nipple-like tip, distal half of ventral surface with row of 5 long filiform esthetascs and 4 subterminal pinnate setae, dorsal surface with subterminal clump of thin naked setae; flange on distal article of peduncle with fewer teeth.

Remarks.—Differences between *P. belizensis* and *P. longipes* are very subtle. Since previous systematic descriptions of *P. longipes* are very generalized and the characteristics defining individual species of *Paranebalia* have not been as well established as they have for *Nebalia* (Dahl 1985), I have noted only the most obvious differences between these two western Atlantic species. Some of the characteristics mentioned may not be of taxonomic value. However, they do differ consistantly from previous descriptions (Willemoes-Suhm 1875, Thiele 1904, Brattegard 1970, Wakabara 1976) and from *Paranebalia* (cf.) *longipes* specimens collected in the Florida Keys (Modlin, personal collection).

Six distinct differences in character structure of *P. belizensis* and *P. longipes* are shown in Table 1. In addition to these there is a consistent difference in total length between *P. belizensis* and *P. longipes*; *P. longipes* is about 60% larger than *P. belizensis*. However, the use of total length as a defining characteristic is questionable because neither Willemoes-Suhm (1875) nor Brattegard (1970) defined their total length measurements. Additionally, total length measurements tend to vary due to the expansion or contraction of the body during fixation and preservation. A more reliable measure might be the carapace length (C.L.). A highly significant ($P \ll 0.001$) relationship exists between the carapace length of *P. belizensis* and its total length (T.L.). The least squares linear regression, T.L. = 2.04(C.L.) + 0.03, defines this relationship (correlation coefficient = $r^2 = 0.97$, $n = 102$).

Figure 1B depicts two subterminal spines projecting from the rostrum. Two spines do

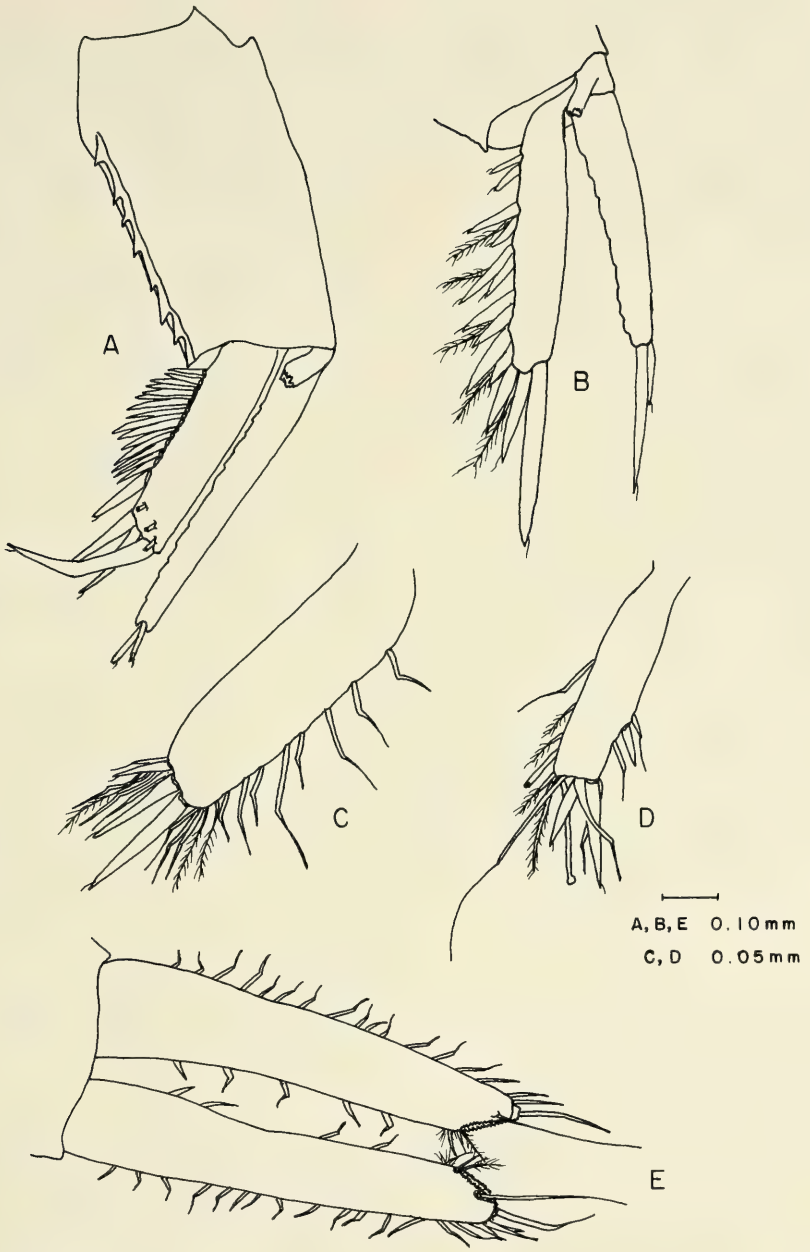


Fig. 4. *Paranebalia belizensis,* new species: A, Pleopod 1; B, Exopod and endopod of pleopod 4; C, Pleopod 5; D, Pleopod 6; E, Furca. Female, 3.3 mm.

exist on the drawn specimen and on others observed, but these spines are so closely superimposed upon each other that on most specimens they are difficult to distinguish separately without high-power phase contrast microscopy. Consequently, all descriptions to date indicate only a single spine. The presence of the second spine may indicate a premolt condition. However, a prominent ventral subterminal keel is pres-

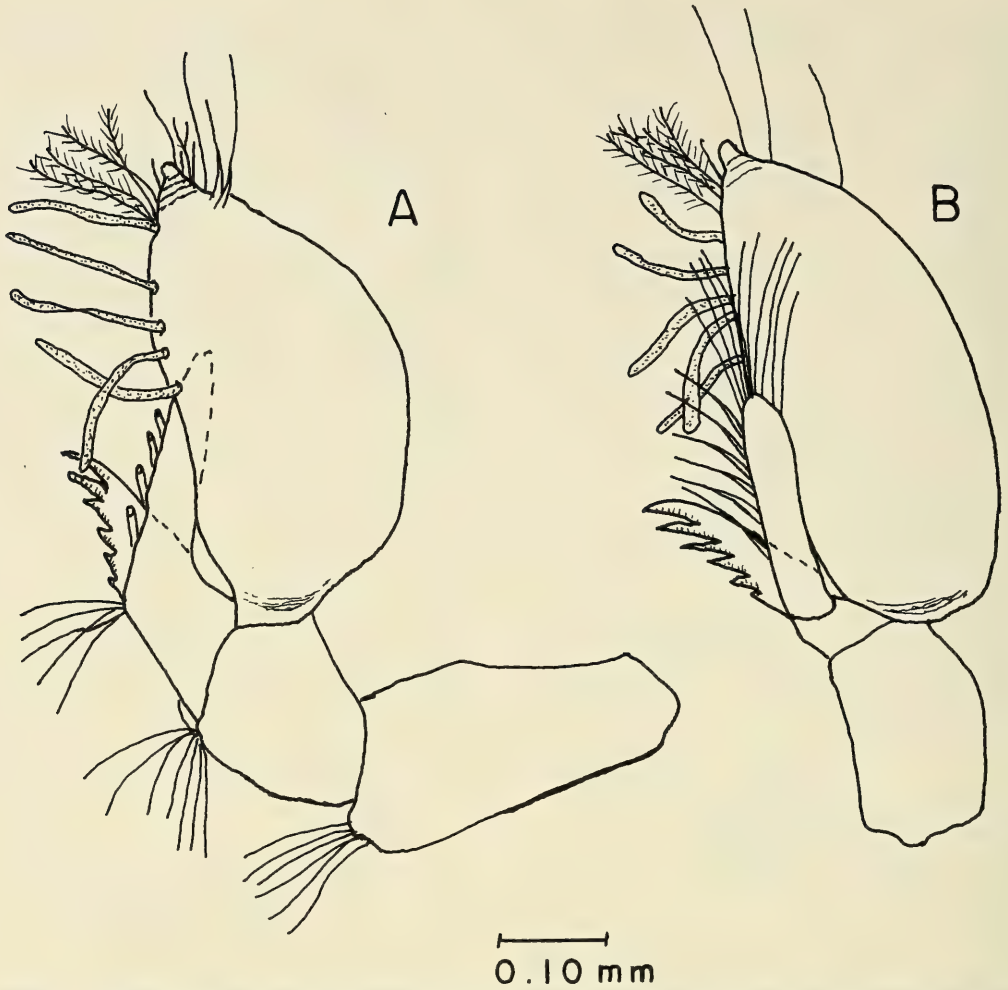


Fig. 5. *Paranebalia belizensis,* new species: A, Antennule, lateral view; B, Antennule, medial view. Male, 2.1 mm.

Table 1.—Characters distinguishing *P. belizensis* from *P. longipes.*

Character	*P. belizensis*	*P. longipes*
Antennule, 4th article, teeth in flange	7–10	10–12
Antennule flagellum, articles	6	7
Antennal flagellum, articles	5	9
Maxilla, endopod, proximal/distal lengths of articles	0.5	0.8
Length of teeth on posterior margins of pleonites 6 and 7	20 μm	33 μm
Setation on margins of furca	sparse	dense

ent on the rostrum of *P. longipes* but not on *P. belizensis.* Two prominant lateral spines consistantly occur on the 3rd article of the antennae of all size of *P. belizensis.* Plate IV, figure 7 published by Willemoes-Suhm (1875) depicts only one spine on this article, but figure 1C of Brattegard (1970) shows two. Specimens from the Florida Keys (R. Modlin, personal collection) are variable, some have one and others two. This difference does not seem to be size dependent.

The habitat of the two species differ. Although both appear to prefer the quiet wa-

ters of isolated or enclosed bays, *P. belizensis* was almost exclusively collected with the algae *Halimeda* growing on proproots of the red mangrove tree. Bottom sediments in the bay inhabited by *P. belizensis* are composed of soft, flocculant organic silt. The habitat of *P. longipes* ranged from a shell-coral rubble substrate in Harrington Sound, Bermuda (Willemoes-Suhm 1875) to calcareous muds, sand and *Thalassia* in the Bahama Islands and Florida Keys (Brattegard 1970, Modlin, personal observation). Although a variety of *Halimeda* spp. do occur in the communities sampled by other authors, the exact micro-habitat *P. longipes* prefers is unknown. Collections of Willemoes-Suhm (1875), Brattegard (1970) and others were made with epibenthic sledges or dredges, while all my observations and collections were made in situ snorkeling gear or SCUBA.

Ecological notes.—Specimens of *P. belizensis* were collected from different locations in the Twin Cays archipelago, but the species was almost exclusively associated with beds and suspended clumps of the algae *Halimeda.* Few specimens were collected from clumps of *Caulerpa racmosa.* Based on abundance, the type habitat is an isolated bay identified as the Lair. This is a small (surface area about 0.3 ha), shallow (average depth about 1.0 m) bay completely surrounded by red mangrove trees, *Rhizophora mangle. Paranebalia belizensis* is more abundant in the lush clumps of *Halimeda* suspended from the proproots at the origin of the single narrow channel (width about 12 m) that allows the exchange of Lair water with open water. Lair water is highly eutrophic and contains much suspended particulate material flushed from the surrounding mangrove swamp during ebb tide. Wave actions are limited to ripples and moderate currents are tidally generated. Surface salinity ranges from 20‰ after rain to 40‰; temperature ranges from 24°C in December to 38°C in July. A complete description of the Twin Cays habitats can be found in Rutzler and Feller (1987/88) and Modlin (1990).

Etymology.—Named for Belize, the country in which *P. belizensis* was first collected.

Acknowledgments

I would like to extend my appreciation to the following scientists: Patricia A. Harris for her assistance in collecting, sorting and measuring specimens, Frank Ferrari for his encouragement and many useful comments during the project, Professor Erik Dahl for his discussions and help on the taxonomy of Leptostraca, and Dr. Eric Hallberg for producing the SEM photograph. I would also like to thank Dr. Tom Bowman and other reviewers for providing comments that greatly improved this manuscript. Funding for this project was obtained through a Mini-Grant from the Research Center of the University of Alabama in Huntsville, and from a short-term fellowship awarded by the Smithsonian Institution's Caribbean Coral Reef Ecosystem Program (CCRE), which is partly supported by the Exxon Corporation. This is contribution number 304 from the CCRE, Smithsonian Institution.

Literature Cited

Brattegard, T. 1970. Marine biological investigations in the Bahamas 13. Leptostraca from shallow water in the Bahamas and southern Florida.—Sarsia 44:1–7.

Clark, A. E. 1932. *Nebaliella Caboti* n. sp., with observations on other Nebaliacea.—Transactions of the Royal Society of Canada, Series 3, 26: 217–235.

Dahl, E. 1985. Crustacea Leptostraca, principles of taxononmy and a revision of European shelf species.—Sarsia 70:135–165.

Modlin, R. F. 1990. Observations on the aggregative behavior of *Mysidium columbiae,* the mangrove mysid.—Marine Ecology 11:263–275.

Rutzler, K., & C. Feller. 1987/88. Mangrove swamp communities.—Oceanus 30(4):16–24.

Sars, G. O. 1887. Report on the Phyllocarida collected by H.M.S. *Challenger* during the years 1873-76.—Challenger Scientific Reports–Zoology 14:1–38.

Thiele, J. 1904. Die Leptostraken.—Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899, 8:1–26, pl. I-IV.

Verrill, A. E. 1923. Crustacea of Bermuda; Schizopoda, Cumacea, Stomatopoda, and Phyllocarida.—Transactions of the Connecticut Academy of Arts and Sciences 26:181–211, pl. 49–56.

Wakabara, Y. 1976. *Paranebalia fortunata* n. sp. from New Zealand (Crustacea, Leptostraca, Nebaliacea).–Journal of the Royal Society of New Zealand 6(3):297–300.

Willemoes-Suhm, R. v. 1875. On some Atlantic Crustacea from the "Challenger" Expedition.–Transactions of the Linnean Society of London, Series 2, Zoology 1:23–59, pl. 6–13.

Department of Biological Sciences, The University of Alabama in Huntsville, Huntsville, Alabama 35899.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 613–619

A SCANNING ELECTRON MICROSCOPE STUDY OF THE BUCCAL COMPLEX OF *METAPENICULUS ANTOFAGASTENSIS* (COPEPODA: PENNELLIDAE)

Raúl Castro Romero and Hernán Baeza Kuroki

Abstract.—The buccal complex for the copepodite, chalimus and adult stages of *Metapeniculus antofagastensis* Castro & Baeza, 1985 is examined and described with the aid of the scanning electron microscope (SEM). The junction between the labium and labrum of the buccal cone at the copepodite stage is shown to be affected by the insertion of the edges of the former between the dorsal and the ventral plates derived from the latter and linked together by a vertical bridge. The formation of the proboscis, following the process of metamorphosis, results in the displacement of the buccal area from the ventral surface of the cephalothorax and from the second maxillae, which remain in their original position on that surface. The intrabuccal armature is described, as is the mandible at different developmental stages. Differences in the morphology of the buccal region of *Peniculus* and *Metapeniculus* are described. Reference is made also to the genus *Ophiolernaea.*

The buccal area of the copepods parasitic on fishes is still inadequately known. Kabata (1974) described the structure of the buccal tube with its associated musculature, as well as the oral appendages and the mode of feeding of *Caligus* (Caligidae), an ectoparasite genus. A similar description was published for the genus *Lepeophtheirus* by Boxshall (1984). Several authors studied the oral region of mesoparasitic (Kabata 1979) copepods belonging to the family Pennellidae. Gooding & Humes (1963) described the buccal area of *Haemobaphes cyclopterina* and John & Nair (1973) that of *Lernaeenicus hemirhamphi* and discussed their functional morphology. Kabata (1979) gave a general account of this area in Poecilostomatoida and commented also on the structure of the buccal tube of Pennellidae. Recently, Chandran & Nair (1988) gave an account of the functional morphology of this area in *Pseudocharopinus narcinae.*

In spite of these publications, the buccal tube and the intrabuccal armature is still inadequately known, because this structure is very small and difficult to study in detail, specially in the pennellid copepods.

In their search for some structural details that could throw new light on the taxonomy of the Pennellidae, the authors studied the buccal complex of *Metapeniculus* Castro & Baeza, 1985 and compared it with that of *Peniculus* von Nordmann, 1832. This paper illustrates and discusses the results of this study.

Methods.—Specimens of *M. antofagastensis,* copepodites, chalimus and adult, were collected from their host fish (*Anisotremus scapularis*), both juvenile and adult. Some fish were taken from their natural environment, while others were reared in a laboratory. The copepods were washed in sea water that was filtered through a millipore filter. They were rinsed in 1M urea to remove fish mucus from the attached specimens, fixed in gluteraldehyde (4%). They were dehydrated in ethanol, critical point dried and then coated with gold or silver, observed and photographed under an Autoscan or Jeol Scanning Electron Micro-

scope at 20 Kv. Light microscopy drawings were made with the aid of a camera lucida.

Results

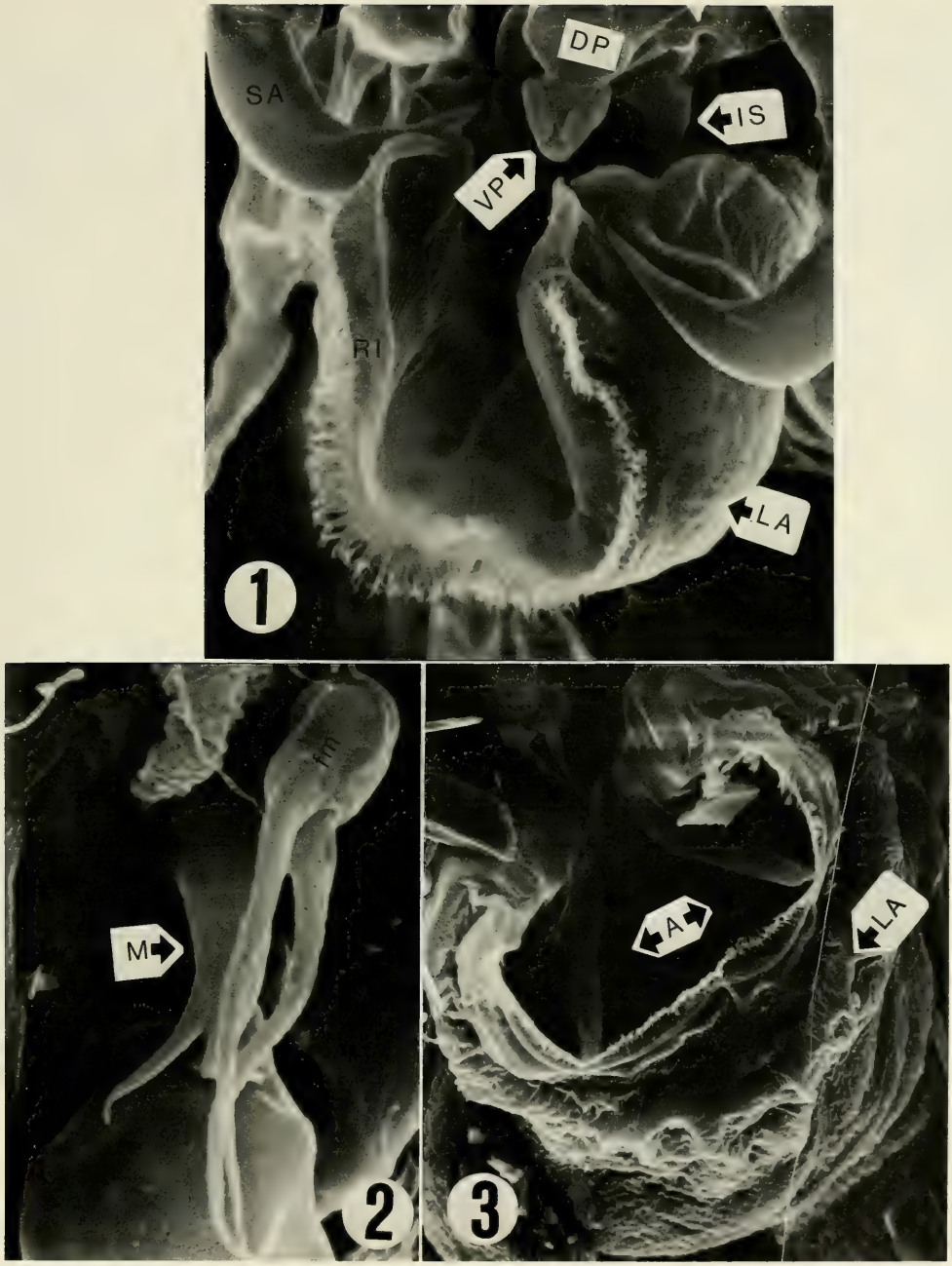
Copepodite (Figs. 1, 2).—The buccal tube (Fig. 1) is formed by both the labium and labrum. The former forms most of the circumference of the tube and bears a fringe of setules at its distal end. The latter is a subtriangular plate, connecting with subcylindrical plate by means of a vertical bridge. Two intrabuccal stylets are present on the inner surface of the labrum near its distal end. The stylets are short, robust and surmounted by a single setiform process. The first maxilla (Fig. 2) is located at the base of the labium. It has the usual pennellid structure. Its exopod is a single seta with a robust base, whereas its endopod carries two long setae. Posteromedial and close to the first maxilla is the mandible, which is an unsegmented stylet with a bifid apex (Fig. 2). The second maxilla is bi-segmented, and is situated posterior to the labrum. Its first segment (=lacertus) and second segment (=brachium) are unarmed. The distal claw carries several spines apically.

Chalimus I and III (Figs. 3–7).—At the first chalimus stages (Fig. 3) the anterior inner surface of the labium is produced into two prominent plate-like swellings (Fig. 3). At the third chalimus stage (Figs. 4, 5) the structure of the buccal cone and tube approaches its definitive condition; the labrum and labium are linked at their distal ends. The upper margin of the labium are inserted between the subtriangular dorsal plate (dp) and subcircular ventral plate (vp) (Fig. 6). At this stage the projections of the inner surface of the labium and the intrabuccal armature of the tube reach their definitive shape (Fig. 7) (Chalimus III is the juvenile stage for this genus). The mandible enters the buccal tube through an opening at the junction of the labium and labrum. Other appendages retain their original position.

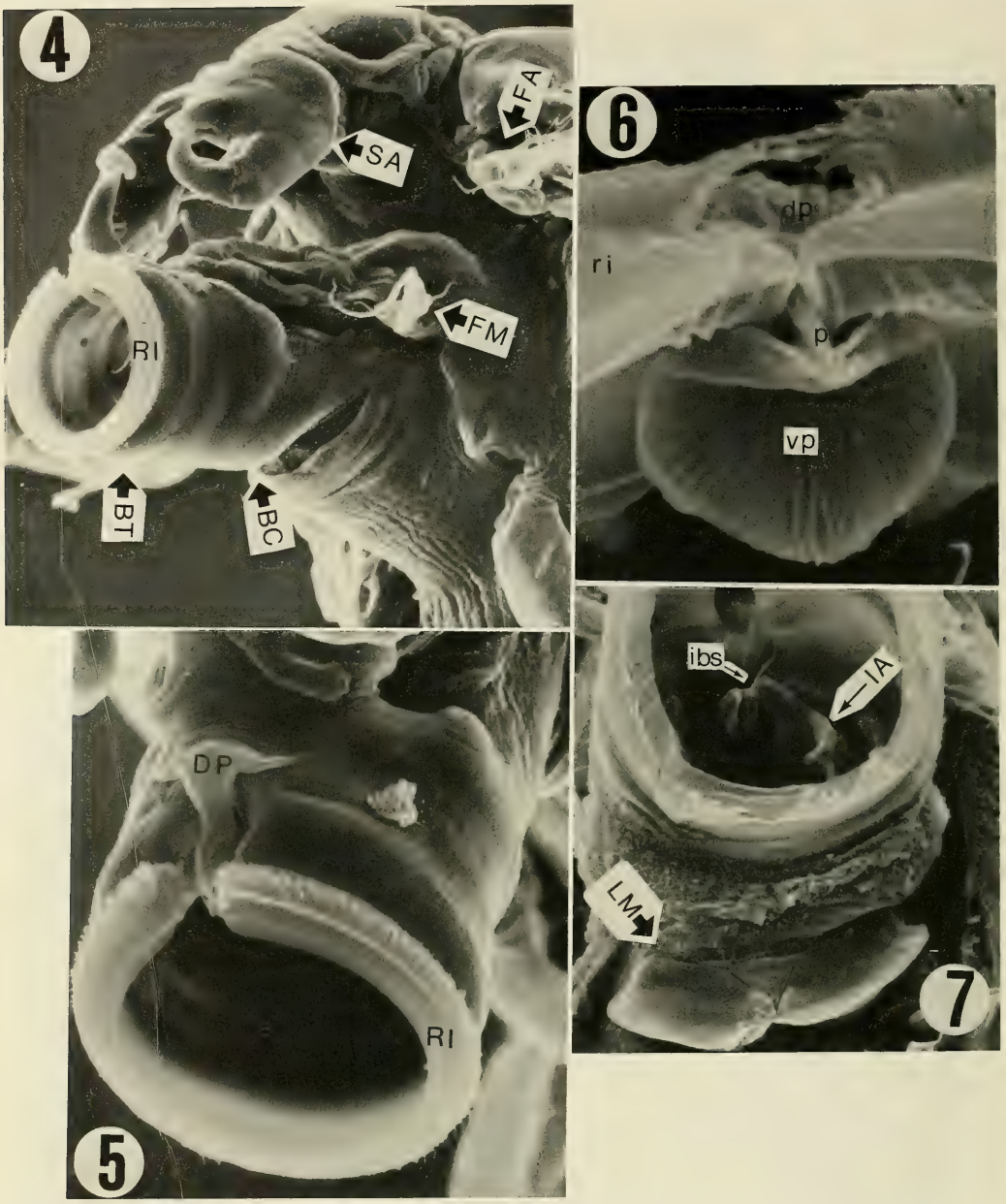
Adult (Figs. 8–11).—The peribuccal area is changed due to the development of a proboscis that pushes the small buccal cone and tube away from the surface of the cephalothorax (Fig. 8). The labrum is now greatly reduced and simple, whereas the labium, which forms most of the buccal tube, consist of three heavily sclerotized rings and is armed with a distal ring of setules. The distolateral surface of the buccal cone bears several microvellosities (Fig. 9, mi). The mandible is difficult to study due to its small size. As far as can be seen, in the adult copepod it is a simple stylet, devoid of dentition. The second maxilla remains at its original position close to the base of the proboscis. The intrabuccal structure has the appearance of two long, wide laminae (Figs. 3, 10, 11) arising from the base of the labium (that is starting from the buccal cone area) with some folding near their tips (Fig. 10, ia), and reaching the buccal opening when the buccal tube is contracted.

Discussion

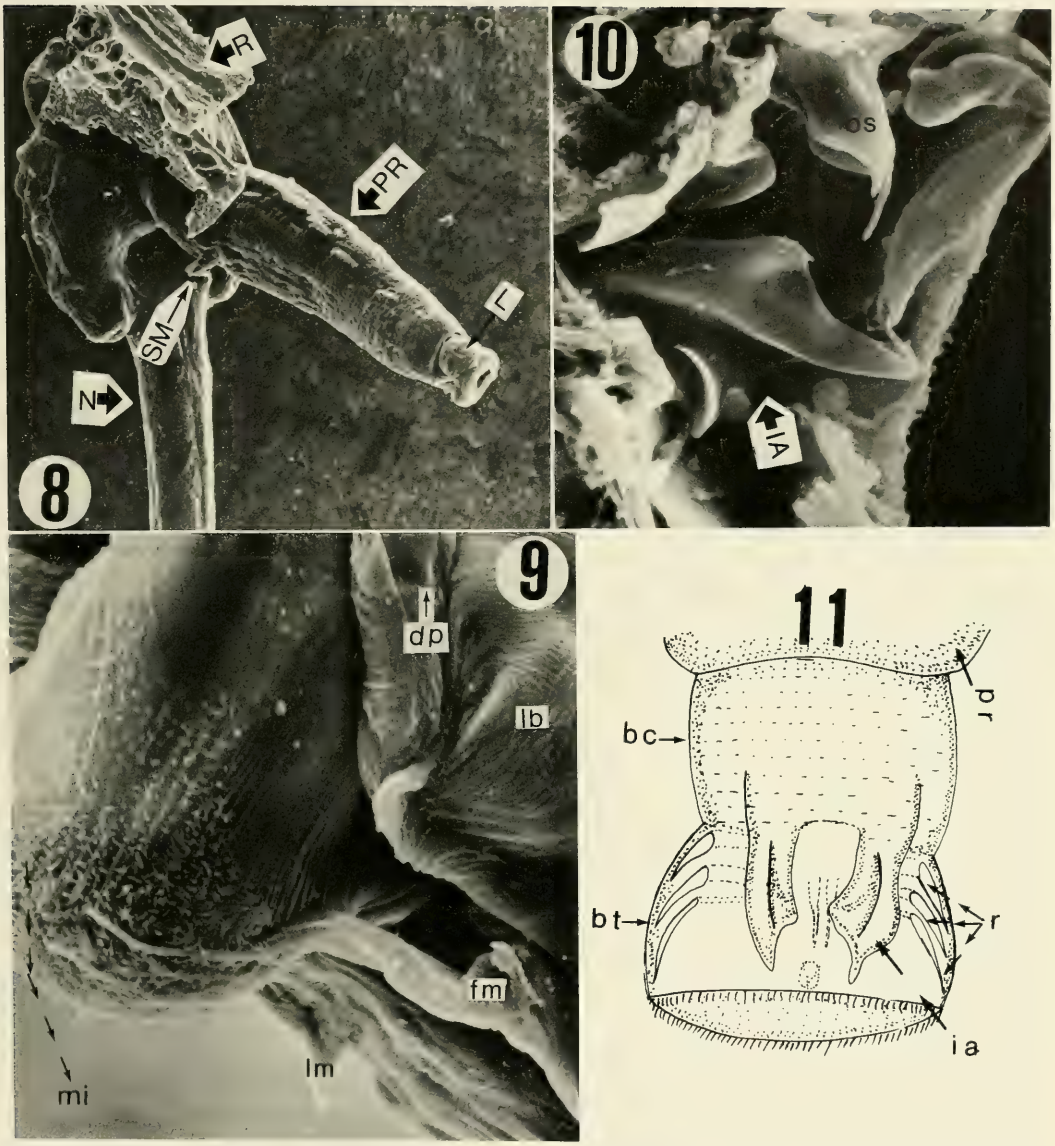
The buccal apparatus of Pennellidae consists of the cone and tube, the former formed by the fusion of the labrum and labium (Kabata 1979). It has now been recognized that the labrum produces a ventral plate (cuticular process of Gooding & Humes 1963; dorsal plaque of Kabata 1979). Gooding & Humes (1963), suggested that the plaque fused with the labium. This would prevent the tube from telescoping to any appreciable extent, although Kabata postulated that the pennellid tube can telescope. The structure of the buccal tube of *Metapeniculus* supports Kabata's assertion. The telescoping (of the buccal tube) is made possible due to the lose insertion of the distal upper margin of the labium, between the dorsal and ventral plates derived from the labrum, allowing free movement of the labium. The buccal tube, supported by three incomplete sclerotized rings, is common for all genera of Pennellidae. While in the majority of these



Figs. 1–3. Copepodite and chalimus I of *Metapeniculus antofagastensis*. 1. Copepodite, frontal view of the buccal area, showing the labium, and the dorsal and ventral plates. 720× (LA = labium, DP = dorsal plate, IS = intrabuccal stylet, SA = second antenna, VP = ventral plate, RI = rim).
2. Copepodite, detail of the first maxilla and mandible. 1730× (fm = first maxilla, M = mandible). 3. Chalimus I, detail of the labium, showing the plate-like swellings. 600× (A = plate-like swellings, LA = labium).



Figs. 4–7. Chalimus III and premetamorphosis female of *Metapeniculus antofagastensis*. 4. Chalimus III, buccal area, lateral view. 400× (BT = buccal tube, BC = buccal cone, FA = first antenna, FM = first maxilla, SA = second antenna). 5. Chalimus III, buccal tube, dorsal view, showing the dorsal plate position. 800× (RI = rim, DP = dorsal plate), 6. Chalimus III, detail upper margin of the rim showing the insertion of the labium between the dorsal and ventral plates. 400× (ri = margin, vp = ventral plate, dp = dorsal plate, p = bridge). 7. Premetamorphosing female, showing the intrabuccal armature. 400× (ibs = intrabuccal stylet, IA = intrabuccal armature, LM = lamina, RI = rim).



Figs. 8–11. Adult female of *Metapeniculus antofagastensis*. 8. Adult female, cephalic area, showing the proboscis and buccal area. 52× (PR = proboscis, L = labrum, Sm = second maxilla, N = neck, R = fin ray fragment of host fish). 9. Buccal tube detail showing the microvellosities (MI = microvellosities, dp = dorsal plate, lm = lamina). 10. Detail of plate-like swelling (= intrabuccal armature) in a buccal tube longitudinal section. 800× (IA = intrabuccal armature, ibs = intrabuccal stylet). 11. Detail of the buccal area, showing the intrabuccal armature as seen by transparence (ia = intrabuccal armature, bt = buccal tube, bc = buccal cone, pr = proboscis,ri = rings of the buccal tube).

genera the buccal area is situated close to the ventral surface of the cephalothorax (i.e., a short buccal area in *Peniculus* and *Lernaeenicus*) in *Metapeniculus* it is displaced away from it as the consequence of the development of a prominent proboscis, resulting from the activity of the oral development centre (Kabata 1979). The length of the proboscis is exceeded only by that of *Ophiolernaea* Shiino, 1958. Boxshall (1986)

pointed out that *Peniculus elongatus* shows an incipient proboscis, indicative of a tendency towards the elongation of a proboscis in this family.

The existence of a prominent proboscis in *Metapeniculus* supports Boxshall's view. Although the genera *Peniculus* and *Metapeniculus* share similar attachment sites on their respective hosts the relative lengths of their proboscis differ considerably. The position of the second maxilla also varies between pennellid genera. In *Metapeniculus* it remains at its original position at the base of proboscis, but in *Ophiolernaea* it migrates with the buccal area to the tip of its extraordinarily long proboscis close to the first maxilla (cf. Ho 1966: figs. 25–27).

The buccal apparatus was hitherto believed to consist of the mandible, first and second maxillae and intrabuccal stylets. This study disclosed the presence of another component of this apparatus, the two long plate-like swellings derived from the proximal part of the inner surface of the labium. They are very difficult to observe with the aid of a low magnification and can only be detected in specimens made translucent by treatment with lactic acid and observed under higher magnification. The laminae are already present in the copepodite stage and complete their development at the final chalimus stage. By eroding the host tissue the laminae are probably able to supplement the function of the mandible, especially when the latter is short and weak as in *Metapeniculus.* The shape of the armature appears to be different in *Metapeniculus* and *Peniculus.* (Their shape for the latter of these genera is now being examined by the authors.)

The pennellid mandible is usually bipartite and armed with teeth, e.g., in *Lernaeocera* (see Kabata 1962) and in *Haemobaphes* (see Gooding & Humes 1963). The mandible of *Metapeniculus,* in contrast, is unsegmented, bifid at the copepodite stage and apparently undivided at the apex and devoid of teeth in the adult.

The structure of the adult mandible, however, requires further study. In this respect also, there exist clear differences between *Peniculus* and *Metapeniculus* in these morphological details. Further study of the buccal region might disclose differences of a similar kind in different genera of the family. The knowledge of these differences might lead to a better understanding of the functional morphology of this area and of the evolutionary trends exhibited by the pennellid copepods.

Acknowledgments

Special thanks are extended to the staff of Electron Microscopy of the Universidad de Concepción, and Universidad Católica del Norte (Sede Coquimbo), for their technical assistance and to all those people who helped us collect samples, and to anonymous reviewers who improved the final manuscript. This study represents a portion of a project sponsored by FONDECYT 0069/88.

Literature Cited

Boxshall, G. A. 1984. The comparative anatomy of the feeding apparatus of representative of four orders of copepods.—Proceedings of the Second International Conference on Copepoda.—Syllogeus 58:158–168.

———. 1986. A new genus and two new species of pennellid (Copepoda: Siphonostomatoida) and an analysis of evolution within the family.—Systematic Parasitology 8:215–225.

Castro, R., & H. Baeza. 1985. *Metapeniculus antofagastensis* gen. et sp. nov. (Copepoda: Pennellidae) parasitic on two inshore fishes of Antofagasta, Chile, South Pacific.—Crustaceana 49: 22–29.

Chandran, A., & N. B. Nair. 1988. Functional morphology of the mouth tube of the lernaeopodid *Pseudocharopinus narcinae* (Pillai, 1962) (Copepoda: Siphonostomatoida).—Hydrobiologia 167:629–634.

Ho, J. S. 1966. Three species of Formosan copepods parasitic on fishes.—Crustaceana 11:163–177.

Gooding, R., & A. G. Humes. 1963. External anatomy of the female *Haemobaphes cyclopterina* a copepod parasite of marine fishes.—The Journal of Parasitology 49(4):663–667.

John, S. E., & N. B. Nair. 1973. Structure of the

mouth tube and method of feeding in *Lernaeenicus hemirhamphi* Kirtisinghe, a parasitic copepod.—Zoologischer Anzeiger 190(1/2):35–40.

Kabata, Z. 1962. The mouth and the mouth parts of *Lernaeocera branchialis* (L), a parasitic copepod.—Crustaceana 3:311–317.

———. 1974. Mouth and mode of feeding of Caligidae (Copepoda), parasites of fishes, as determined by light and scanning electron microscopy.—Journal of the Fisheries Research Board of Canada 31:1583–1588.

———. 1979. Parasitic Copepods from British fishes. Ray Society, London, 468 pp.

Nordmann, A. von. 1832. Mikrographische Beitrage Zur Naturgeschichte der wirbellosen. Thiere., G. Reimer. Berlin 2:1–150.

Shiino, S. 1958. Copepods parasitic on Japanese fishes. 17 Lernaeidae.—Report of Faculty of Fisheries, Prefectural University of Mie 3(1):75–100.

Universidad de Antofagasta, Facultad de Recursos del Mar, Departamento de Acuicultura, Casilla 170, Antofagasta, Chile.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 620–621

CALANUS EUXINUS, NEW NAME, A REPLACEMENT NAME FOR *CALANUS PONTICUS* KARAVAEV, 1894 (COPEPODA: CALANOIDA)

Kuni Hulsemann

Abstract.—The history of *Calanus ponticus* Karavaev, 1894 is presented and the new replacement name, *Calanus euxinus,* proposed.

The first author to distinguish the members of the genus *Calanus* Leach, 1819 living in the Black Sea from those found elsewhere was Karavaev (1894:37, pl.3, figs. 1–18) (also transliterated Karawaiew). He named this population *Calanus finmarchicus* Günner var. *pontica.* Thereafter, he became aware of Giesbrecht's (1892) description of *C. finmarchicus* Gunnerus (p. 89) from the Mediterranean Sea which led Karavaev to re-examine his specimens and to compare these and additional specimens from the Black Sea to this description. The supposed differences upon which Karavaev had based the distinctiveness of the Black Sea population did not hold up; consequently, Karavaev (1895:121) withdrew his var. *pontica.*

Claus (1863:171) described a close relative of *Calanus finmarchicus* from the southern North Sea choosing to use for it the genus-group name *Cetochilus* Roussel de Vauzème, 1834 over the earlier *Calanus* Leach, thus disagreeing with Dana (1849: 11) who had indicated the possible synonymy of *Cetochilus* with *Calanus.* The species to which Claus chose to apply the name *Calanus* are now divided among the genera *Paracalanus* Boeck, 1865, *Calocalanus* Giesbrecht, 1888 and *Clausocalanus* Giesbrecht, 1888. Claus named the new species from the southern North Sea *Cetochilus helgolandicus.* Nevertheless, Boeck (1865:230) included *Cetochilus* in *Calanus* Leach and synonymized the species-group name *helgolandicus* with *finmarchicus.* The prominent authors Brady (1883:30) and Giesbrecht (1892:89) agreed with this synonymy. It is, therefore, not surprising that Karavaev (1894, 1895), too, considered it to be correct. However, Sars (1901:10, 12), while recognizing the genus-group name *Calanus* as valid, pointed out the separate status of *C. finmarchicus* and *C. helgolandicus.*

In various studies on morphology, distribution and systematics of *Calanus finmarchicus* s. l. Jashnov (1955, 1957, 1970) discussed differences between *C. finmarchicus* s. s. and *C. helgolandicus.* In the latter species he distinguished the population in the Black Sea as the new var. *ponticus* (1955: 1216, 1957:194), later raised to subspecies *C. h. ponticus* (1970:204). Kovalev (1969: 147) and Kovalev et al. (1975:195) presented further supporting evidence for the distinctiveness of the Black Sea specimens.

In their paper on geographical variation of *Calanus helgolandicus* s. l. Fleminger & Hulsemann (1987:76) proposed to give the Black Sea population the rank of species and the name *C. ponticus* Karavaev. Unknown to these authors Krichagin (1873:403) had already introduced the name *Calanus ponticus* for a species from the Black Sea. Krichagin used *Calanus* sensu Claus, 1863; his species belongs to the genus *Paracalanus* Boeck. Claus (1863:172) stated that the genus to which Leach (1819:539) first applied the name *Calanus* in no way conformed to the diagnosis he himself was giving for the genus. In spite of this statement his diagnosis and description are here deemed not to constitute the establishment of a nominal genus, but rather an erroneous assignment

of four species to *Calanus*. Consequently, *Calanus* sensu Leach and *Calanus* sensu Claus are not homonyms. The name *ponticus* Jashnov is a junior synonym of *ponticus* Karavaev; both names are junior primary homonyms of *ponticus* Krichagin (Article 57(b), International Code of Zoological Nomenclature) and hence invalid. A new name for *ponticus* Karavaev is required.

I hereby propose *Calanus euxinus* as a new replacement name for *C. ponticus* Karavaev, 1894. The species-group name is taken from the Greek euxeinos meaning hospitable, a classical epithet of the Black Sea.

In an obituary for A. Fleminger (Ferrari 1988:492) the authorship of *Calanus ponticus* was erroneously ascribed to Fleminger & Hulsemann, 1987.

Acknowledgments

I am grateful to Drs. J. W. Reid and T. E. Bowman, both National Museum of Natural History, Smithsonian Institution, Washington, D.C., for drawing my attention to the homonymy, and to T. E. Bowman for his valuable help with literature and discussion.

Literature Cited

Boeck, A. 1865. Oversigt over de ved Norges Kyster iagt-tagne Copepoder hendørende til Calanidernes, Cyclopidernes og Harpactidernes Familier.—Forhandlinger i Videnskabs-Selskabet i Kristiania 1864:226–282.

Brady, G. S. 1883. Report on the Copepoda collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–1876. Zoology 8, 23:1–142 + pls. 1–55.

Claus, C. 1863. Die frei lebenden Copepoden. Leipzig. Wilhelm Engelmann, 230 pp. + pls. 1–37.

Dana, J. D. 1849. Conspectus Crustaceorum quae in Orbis Terrarum circumnavigatione, Carolo Wilkes e Classe Reipublicae Foederatae Duce, pt. 2.—Proceedings of the American Academy of Arts and Sciences 2:9–61.

Ferrari, F. D. 1988. Abraham Fleminger (1925–1988).—Journal of Crustacean Biology 8:490–492.

Fleminger, A., & K. Hulsemann. 1987. Geographical variation in *Calanus helgolandicus* s. l. (Copepoda, Calanoida) and evidence of recent speciation in the Black Sea population.—Biological Oceanography 5:43–81.

Giesbrecht, W. 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel.—Fauna und Flora des Golfes von Neapel 19:1–831 + pls. 1–54.

Jashnov, V. A. 1955. Morphology, distribution and systematics of *Calanus finmarchicus* s. l.—Zoologicheskii Zhurnal 34(6):1210–1223.

———. 1957. Comparative morphology of the species of *Calanus finmarchicus* s. l.—Zoologicheskii Zhurnal 36(2):191–198.

———. 1970. Distribution of *Calanus* species in the Seas of the Northern Hemisphere.—Internationale Revue der Gesamten Hydrobiologie 55(2):197–212.

Karavaev, V. 1894. Contributions to the Crustacean pelagic fauna of the Black Sea.—Kiev. Universitet. Obshchestvo estestvoispitatelei, Zapiski 13(1):35–61 + pls. 3–5.

———. 1895. Contributions to the copepod fauna of the Black Sea.—Kiev. Universitet. Obshchestvo estestvoispitatelei, Zapiski 14(1):117–174 + pls. 1–3.

Kovalev, A. V. 1969. Variability in certain plankton Copepoda (Crustacea) in Mediterranean Sea Basins. Pp. 144–197, 231 *in* Biologiia Moriia 17. Productive-biological processes in the plankton of Southern Seas. Akademiia Nauk Ukrainskoi SSR, Kiev.

———, E. P. Shelukhin, & V. N. Ivanov. 1975. On the taxonomic status of the Black Sea representative of the genus *Calanus* (Copepoda).—Zoologicheskii Zhurnal 54(2):195-199.

Krichagin, N. 1873. Contributions to the knowledge of the fauna of the Black Sea. Copepoda.—Kiev. Universitet. Obshchestvo estestvoispitatelei, Zapiski 3(3):370–429 + pls. 10–14.

Leach, W. E. 1819. Entomostraca. Pp. 524–543 *in* F. Cuvier, ed., Dictionnaire des Sciences Naturelles, volume 14. Paris, Strasbourg.

Roussel de Vauzème, A. 1834. Description du *Cétochilus Australis*, noveau genre du Crustacé branchiopode.—Annales des Sciences Naturelles, Paris 1:333–338.

Sars, G. O. 1901. An account of the Crustacea of Norway. 4. Copepoda, Calanoida, parts I, II:1–28 + pls. 1–16. Bergen Museum, Bergen.

Biologische Anstalt Helgoland, Taxonomy Group, Notkestraße 31, 2000 Hamburg 52, Federal Republic of Germany.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 622–626

RECORDS OF THE MARINE GENUS *BATHYDRILUS* (OLIGOCHAETA: TUBIFICIDAE) FROM CALIFORNIA, WITH DESCRIPTIONS OF TWO NEW SPECIES

Christer Erséus

Abstract.—*Bathydrilus litoreus* Baker, 1983, *B. parkeri,* new species, and *B. rusticus,* new species, are described from subtidal habitats in southern California. *Bathydrilus parkeri* appears closely related to *B. exilis* Erséus & Davis, 1989, a larger species from Hawaii, but its postclitellar setae are not single-pointed as those of the latter taxon. *Bathydrilus rusticus* resembles *B. torosus* Baker, 1983, an intertidal species from British Columbia, but is discriminated by its much different spermathecae.

Baker (1983) described two intertidal species of *Bathydrilus* Cook, 1970, *B. litoreus* Baker, 1983 (from British Columbia and Washington) and *B. torosus* Baker, 1983 (from British Columbia), which are the only members of this genus recorded from the Pacific coast of North America to date. In the present paper, three species of *Bathydrilus* from offshore localities in southern California are treated. One is *B. litoreus,* the other two are new taxa.

The material originates from (1) the Bureau of Land Management (BLM) Outer Continental Shelf Project in the Southern California Bight, placed at the author's disposal by the Allan Hancock Foundation, University of South California, Los Angeles (courtesy, Dr. J. Kudenov; now at University of Alaska, Anchorage); and (2) the Los Angeles County Sanitation Districts benthic sampling off Los Angeles (courtesy, Dr. T. Parker, Joint Water Pollution Control Plant, L.A. County Sanitation Districts). The worms were stained in paracarmine and mounted whole in Canada balsam prior to examination. Types and other material are deposited at the National Museum of Natural History (USNM), Washington, D.C., and the Los Angeles County Museum of Natural History (LACM), Los Angeles, California.

Bathydrilus litoreus Baker, 1983

Bathydrilus litoreus Baker, 1983:2162–2164, figs. 1, 2A.—Erséus 1990:68–69, fig. 13.

New material.—USNM 136578–136580, 3 specimens from Southern California Bight: 1 from Santa Cruz Island (slope of Santa Crus Basin), 260 m, medium to coarse sand (BLM project Sta. no. 80907); 1 from same area and sediment, but 271 m (BLM project Sta. no. 80908); 1 from same area, but 257 m, medium sand with small pebbles (BLM project Sta. no. 80929). LACM, 3 specimens from Southern California Bight: 1 from Tanner Bank, 96 m, fine sand (BLM project Sta. no. 81505); 1 from same area, but 203 m, coarse sand with shell (BLM project Sta. no. 81827); and 1 from San Nicholas Island, 279 m, coarse sand with small rocks (BLM project Sta. no. 84103).

Remarks.—Originally described from intertidal localities in British Columbia and Washington (Baker 1983), this species was recently reported also from subtidal depths (15 m) in Southwestern Australia (Erséus 1990). The new specimens from Southern

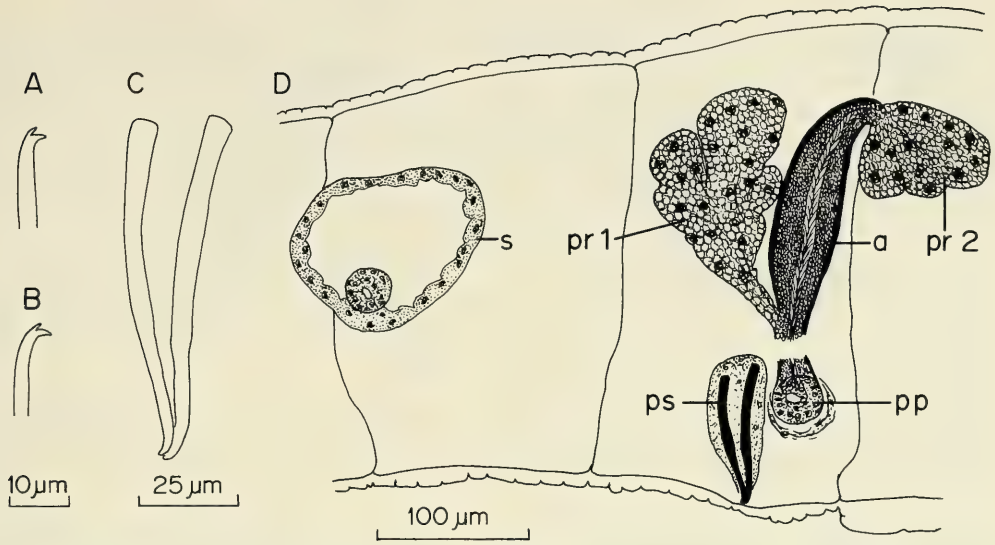


Fig. 1. *Bathydrilus parkeri.* A, Anterior somatic seta; B, Postclitellar somatic seta; C, Penial setae; D, Lateral view of genitalia in segments X–XI. Abbreviations: a, atrium; pp, pseudopenis; pr1, anterior prostate gland; pr2, posterior prostate gland; ps, penial seta; s, spermatheca.

California are from deeper sites, at 96–279 m depth. A brief description of the new material follows:

Length of only complete individual 14.0 mm, about 77 segments; other, incomplete, worms longer, but much stretched. Somatic setae 3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae single-pointed, straight and closely parallel within bundle, 100–140 µm long, 3 per bundle, and enclosed in large, glandular, bilobed sac (see Erséus 1990: fig. 13C). Atria 115–150 µm long, 45–50 µm wide.

With regard to body size, the new worms thus resemble the original B.C./Washington material more than they do the Australian specimens; the latter were 16.5–22.1 mm long with 90–115 segments. The Californian individuals, however, have somewhat smaller penial setae and atria than the previously studied material; in the latter, penial setae were 140–160 µm, atria 170–230 µm long.

In the more northern populations of *B. litoreus,* the penial setae are mostly 2 (occasionally 3–5) per bundle (Baker 1983). In the Australian material there is also some variation in this character, the penial setae mostly 3 (occasionally 2 or 4) per bundle (Erséus 1990). The penial setae of the new material are invariably 3 per bundle.

Distribution and habitat.—California (new record), Washington, British Columbia; also southwestern Australia. Intertidal and subtidal sands, to at least 279 m depth.

Bathydrilus parkeri, new species
Fig. 1

Holotype.—USNM 136573, whole-mounted specimen.

Type locality.—Off Kou radio towers, Palos Verdes Peninsula, Los Angeles, California, 30 m, silty sand (July 1980; Los Angeles County Sanitation Districts benthic sampling station no. 6D).

Paratypes.—USNM 136574, 1 specimen from type locality. LACM AHF 1533, 1 specimen from type locality.

Etymology.—Named for Dr. Thomas Parker (Joint Water Pollution Control Plant, Carson, California), who kindly provided the material.

Description.—Length 10.1–10.9 mm, from about 70 to 78 segments. Width at XI 0.27–0.35 mm. Prostomium elongate. Epidermal glands as large dorsal patches in many segments, well visible in at least one specimen. Clitellum extending over ½X–XII. Somatic setae 40–50 μm long, 2–3 μm thick, 3 per bundle anteriorly, 2 per bundle in postclitellar segments. These setae bifid, with upper tooth shorter and thinner than lower, more pronouncedly so in postclitellar (Fig. 1B) than in anterior segments (Fig. 1A). Penial setae (Figs. 1C; D, *ps*) 2 per bundle, 75–90 μm long, 5–7 μm thick, single-pointed with somewhat curved tips; within bundle, inner ends of setae wider apart than tips. Male pores paired, in line with ventral setae, posteriorly in XI. Spermathecal pores paired in lateral lines, in most anterior part of X.

Pharyngeal glands in IV-VIII(IX), well developed. Some anterior septa, in particular 6/7 and 7/8, thickened, conspicuously muscular. Male genitalia (Fig. 1D) paired. Vas deferens not seen in available material, but appears to enter ectal end of atrium near attachment of anterior prostate gland. Atrium slender and spindle-shaped; erect or somewhat tilted over to posterior, 150–220 μm long, 40–47 μm wide, with 2–3.5 μm thick outer lining of muscles, and ciliated, granulated inner epithelium. Anterior prostate gland attached to ectal end of anterior face of atrium, posterior prostate gland to apex of atrium. Atrium terminating in bulbous, simple, pseudopenis, but details not clear in available material. Spermathecae (Fig. 1D, s) with very short ducts, and oval ampullae, 70–125 μm long, 45-106 μm wide. Lumen of spermathecae with some globules of secretion and an amorphous substance, but no sperm observed (specimens precopulatory?).

Remarks.—*Bathydrilus parkeri* appears closely related to *B. exilis* Erséus & Davis, 1989. The latter, which is known only from Hawaii, also has somewhat curved penial setae with inner ends wider apart than outer tips, heavily muscular anterior septa, and slender, more or less erect atria and somewhat curved penial setae (Erséus & Davis 1989). The posterior setae of *Bathydrilus exilis,* however, are not bifid as those of *B. parkeri* but sharply single-pointed. Moreover, the Hawaiian species is about twice as large (up to at least 26.5 mm, with 149 segments) as the new taxon.

Distribution and habitat.—Known only from type locality near Los Angeles, southern California. Subtidal silty sand, 30 m depth.

Bathydrilus rusticus, new species
Fig. 2

Holotype.—LACM AHF 1527, whole-mounted specimen from type locality.

Type locality.—Tanner Bank, Southern California Bight, 113 m, coarse sand and shells (BLM project Sta. no. 81810).

Paratype.—USNM 136575, specimen from type locality.

Etymology.—Named *rusticus* (Latin for 'simple, plain'), alluding to this species' lack of penial setae.

Description.—Holotype 11.8 mm long, with 67 segments; paratype 9.9 mm, 44 segments. Width at XI 0.23–0.25 mm. Prostomium large, somewhat elongate with rounded tip. Epidermal glands not observed. Clitellum extending over ½X–XII in holotype, poorly developed in paratype. Somatic setae 55–75 μm long, 2.5–3.5 μm thick, 2–3 per bundle anteriorly, 2(3) per bundle in postclitellar segments. Anterior setae (Fig. 2A) bifid, with upper tooth much shorter and thinner than lower. Postclitellar setae with rudimentary upper tooth, or (more commonly?) single-pointed with curved tip (Fig. 2B). Ventral setae of XI (penial setae) absent. Male pores paired, in line with ventral setae, posteriorly in XI. Spermathecal pores paired, immediately ventral to lateral lines, in most anterior part of X.

Pharyngeal glands extending in VIII, but poorly developed. Some anterior septa somewhat thickened, but not conspicuously

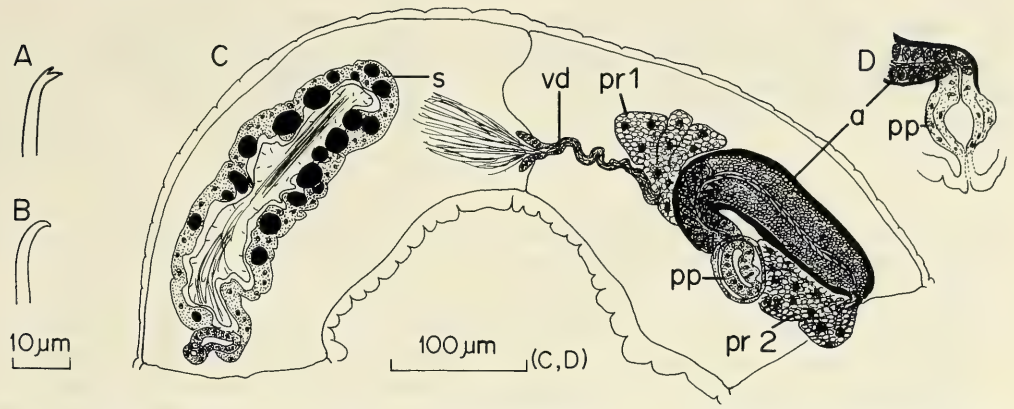


Fig. 2. *Bathydrilus rusticus.* A, Anterior seta; B, Postclitellar seta; C, Lateral view of spermatheca and male genitalia in segments X–XI (one side of holotype); D, Outer end of male duct (other side of holotype). Abbreviations: vd, vas deferens; other abbreviations as in Fig. 1.

muscular. Male genitalia (Fig. 2C, D) paired, partly extending into XII in paratype. Vas deferens inconspicuous, 3–8 µm wide, somewhat coiled, and appars to enter ectal end of atrium near attachment of anterior prostate gland. Atrium slender, tilted over to posterior, 150–230 µm long, 47–50 µm wide, with 2.5–5 µm thick outer lining of muscles, and ciliated, histologically bipartite inner epithelium; ental (longer) part of atrium evenly granulated; granules of ectal (shorter) part aggregated in discrete 'packages'. Anterior prostate gland attached to ectal end of anterior face of atrium, posterior prostate gland to apex of atrium. Atrium terminating into hollow pseudopenial sac (best observed at one side of holotype; Fig. 2D), but details not clear in available material. Spermathecae (Fig. 2C, s) with distinct ducts, 30–45 µm long, about 20 µm wide, and elongate ampullae, 200–260 µm long, 40–75 µm wide. Walls (and parts of lumina?) of spermathecal ampullae with large globules of secretion; each ampulla containing an amorphous substance in which bundled sperm appear to be cemented.

Remarks.—*Bathydrilus rusticus* appears closely related to *B. torosus* Baker, 1983, an intertidal species from British Columbia. Both taxa have setae with much reduced upper teeth, muscular, posteriorly directed atria, and elongate (although morphologically different) spermathecae, but they lack penial setae. According to Baker (1983), the atria of *B. torosus* open to the exterior on the ventral aspect of large papillae; it is possible that these papillae are everted pseudopenes of a kind similar to those present in *B. rusticus* (see Fig. 2D).

It is not clear from Baker's (1983) description whether the thick-walled ectal part of the spermathecae of *B. torosus* is an unusually long spermathecal duct, or whether it is merely a part of the ampulla, but his fig. 3C seems to suggest the former alternative. Be it any way, in *B. rusticus,* the spermathecal ducts are very short and narrow, and clearly set off from the elongate ampullae, and the sperm are arranged in slender bundles inside an amorphous mass in the spermathecae, not in roundish spermatozeugmata (termed "spermatophores" by Baker) as in *B. torosus.*

Distribution and habitat.—Known only from type locality in the Southern California Bight (NE Pacific). Subtidal coarse sand, 113 m depth.

Acknowledgments

I am indebted to Dr. J. Kudenov and Dr. T. Parker, for placing the oligochaete ma-

terial at my disposal; to Ms. Barbro Löfnertz and Mrs. Birgitta Vallander, for technical assistance; and the Swedish Natural Science Research Council, for financial support.

Literature Cited

Baker, H. R. 1983. New species of *Bathydrilus* Cook (Oligochaeta; Tubificidae) from British Columbia.—Canadian Journal of Zoology 61:2162–2167.

Cook, D. G. 1970. Bathyal and abyssal Tubificidae (Annelida, Oligochaeta) from the Gay Head-Bermuda transect, with descriptions of new genera and species.—Deep-Sea Research 17:973–981.

Erséus, C. 1990. The marine Tubificidae and Naididae (Oligochaeta) of Southwestern Australia. Pp. 43–88 *in* F. E. Wells, D. I. Walker, H. Kirkman, & R. Lethbridge, eds., Proceedings of the Third International Marine Biological Workshop: the marine flora and fauna of Albany, Western Australia. Volume 1. Western Australian Museum, Perth, 437 pp.

———, & D. Davis. 1989. The marine Tubificidae (Oligochaeta) of Hawaii.—Asian Marine Biology 6:73–100.

Zoo-tax, Swedish Museum of Natural History, Stockholm, and (postal address): Department of Zoology, University of Göteborg, Box 25059, S-400 31 Göteborg, Sweden.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 627–630

TWO NEW DEEP-WATER SPECIES OF THE GUTLESS GENUS *OLAVIUS* (OLIGOCHAETA: TUBIFICIDAE) FROM BOTH SIDES OF NORTH AMERICA

Christer Erséus

Abstract.—*Olavius tannerensis,* new species, from the continental shelf off California, and *O. rallus,* new species, from off North Carolina, are described. The former is the first member of the genus known from the Pacific coast of North America, the latter the first gutless oligochaete collected at bathyal depths (583 m). Both species have small atria and complex copulatory sacs, but they lack penial setae. They are distinguished from each other by the location of their spermathecal pores.

The gutless oligochaetes, over 50 described species within *Inanidrilus* Erséus, 1979a and *Olavius* Erséus, 1984, are common in shallow marine waters of tropical and subtropical areas. They are particularly well represented in the poorly oxygenated carbonate sands of coral reefs (Giere et al. 1984; Erséus 1984, 1990). Only three species (of *Olavius*) have been found in deeper (>100 m), colder waters. *Olavius tenuissimus* (Erséus, 1979b) and *O. cornuatus* Davis, 1984 occur to at least about 140 m depth on Georges Bank, off Massachusetts in the Northwest Atlantic (Davis 1984, 1985), and *O. macer* Erséus, 1984 was described from a single station at 170 m in the eastern part of the Gulf of Mexico (Erséus 1984).

In the present paper, two additional deep-water species of *Olavius* are described. *Olavius tannerensis,* new species, is the first gutless oligochaete recorded from the Pacific coast of North America, *O. rallus,* new species, the first one from bathyal depths; the latter was found at 583 m off North Carolina (Northwest Atlantic).

Material and Methods

The material of *O. tannerensis* was found in a collection of oligochaetes from the Bureau of Land Management (BLM) Outer Continental Shelf Project in the Southern California Bight, placed at the author's disposal by the Allan Hancock Foundation, University of South California, Los Angeles (courtesy, Dr. J. Kudenov; now at University of Alaska, Anchorage). The specimen of *O. rallus* originates from the Study of Biological Resources on the U.S. South Atlantic Continental Slope and Rise (Blake et al. 1987), supported by contract number 14-12-0001-30064 from the U.S. Department of Interior, Minerals Management Service, to Battelle New England Marine Research Laboratory, Woods Hole Oceanographic Institution, and Lamont-Doherty Geological Observatory (courtesy, Dr. Nancy Maciolek-Blake).

The worms were stained in paracarmine and mounted whole in Canada balsam prior to examination. Types are deposited at the Los Angeles County Museum of Natural History (LACM), Los Angeles, California, and at the National Museum of Natural History (USNM), Washington, D.C.

Olavius tannerensis, new species
Fig. 1A, B

Holotype.—LACM AHF 1528, whole-mounted specimen from Tanner Bank, Southern California Bight, 173 m, coarse sand with shell (BLM project Sta. no. 81828).

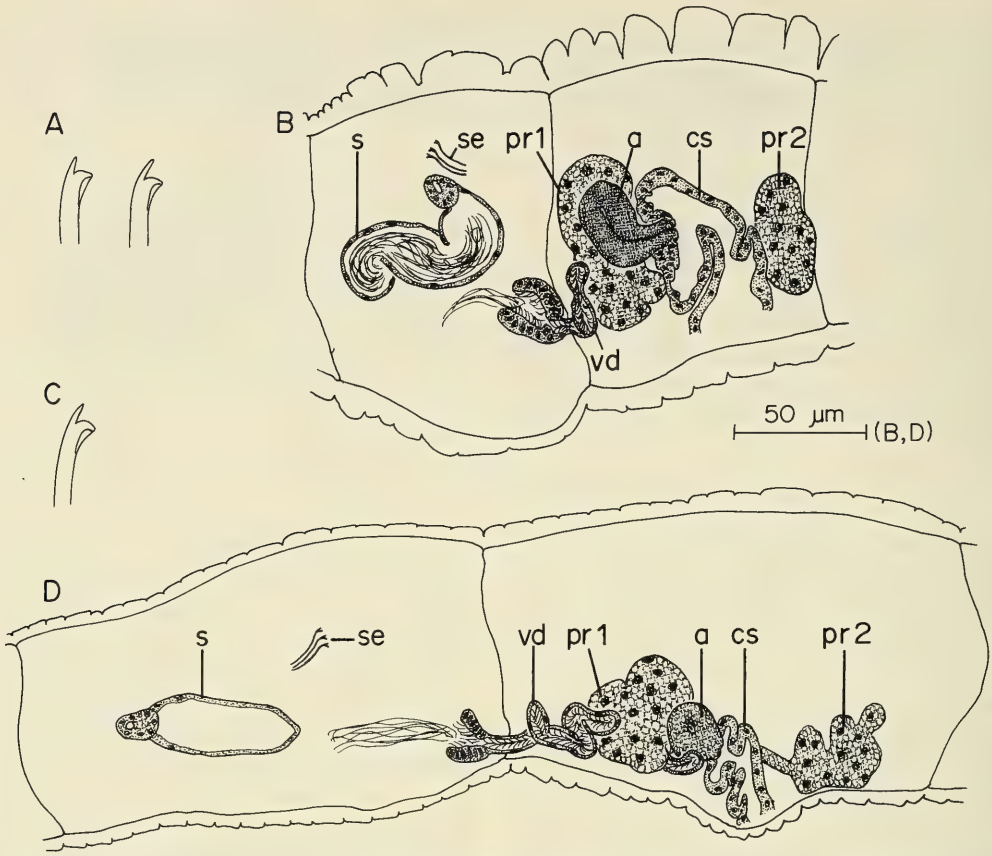


Fig. 1. A, B. *Olavius tannerensis*. A, Free-hand drawing of setae; B, Lateral view of spermatheca and male genitalia in segments X–XI; C, D, *Olavius rallus*. C, Free-hand drawing of seta; D, Lateral view of spermatheca and male genitalia in segments X–XI. Abbreviations.—a, atrium; cs, copulatory sac; pr1, anterior prostate gland; pr2, posterior prostate gland; s, spermatheca; se, setae; vd, vas deferens.

Paratype.—USNM 136576, specimen from type locality.

Etymology.—Named *tannerensis* for the type locality, Tanner Bank.

Description.—Holotype not complete; paratype 5.3 mm long, 46 segments. Width at XI 0.15 mm. Prostomium and pygidium small, elongate with rounded tips. Body round in cross-section. Clitellum extending over ½X–XII. Secondary annulation conspicuous, annuli 5–7 per (postclitellar) segment. Setae (Fig. 1A) bifid, wide subdental ligaments, and with upper teeth variably long but always thinner than lower teeth. Setae 26–37 µm long, 1–2, µm thick, (2)3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae absent. Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pores paired, immediately antero-ventral to dorsal setae in X (see Fib. 1B).

Alimentary canal absent. Male genitalia (Fig. 1B) paired. Vas deferens 5–7 µm wide, longer than atrium; junction with latter not observed. Atrium somewhat curved, pear-shaped, about 30–40 µm long, 21–25 µm wide, with very thin outer lining and thick, granulated inner epithelium, opening into inner part of large, folded copulatory sac. Two prostate glands present, but attachments with atrium not observed. Spermathecae (Fig. 1B, s) with very short ducts,

and elongate, very thin-walled ampullae; latter 70–100 μm long, 20–27 μm wide, containing large random masses of sperm.

Remarks.—As indicated by the small atria, the well developed copulatory sacs, and, in particular, the unusual location of the spermathecal pores near the dorsal setae in segment X, *Olavius tannerensis* is closely related to the northwest Atlantic *O. tenuissimus* (redescribed by Erséus 1990) and *O. finitimus* Erséus, 1990. However, the new species is readily distinguished from these taxa by its lack of penial setae.

See also Remarks for *O. rallus* below.

Distribution and habitat.—Known only from the type locality off southern California, NE Pacific. Subtidal coarse sand, 173 m depth.

Olavius rallus, new species
Fig. 1C, D

Holotype.—USNM 136577, whole-mounted specimen from the continental slope off Cape Lookout, North Carolina, U.S.A., 34°16.2′N, 75°45.8′W, 583 m (November 1983; courtesy N. Maciolek-Blake).

Etymology.—Named *rallus* (Latin for 'thin') for its slenderness.

Description.—Length 7.4 mm, 39 segments. Width at XI 0.13 mm. Prostomium and pygidium small, somewhat triangular. Body round in cross-section. Clitellum extending over ½X–X11. Secondary annulation indistinct. Setae (Fig. 1C) bifid, with subdental ligaments, and with upper teeth thinner and slightly shorter than lower teeth. Setae about 30 μm long, 1–1.5 μm thick, 3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae absent. Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pores paired in line with dorsal setae, in anterior part of X, about mid-way between septum 9/10 and dorsal setae of X (See Fig. 1D).

Alimentary canal absent. Male genitalia (Fig. 1D) paired. Vas deferens 7–9 μm wide, longer than atrium; but junction with latter not observed. Atrium small, somewhat pear-shaped, about 25 μm long, about 20 μm wide, with very thin outer lining and thick, granulated inner epithelium, opening into inner part of small, folded copulatory sac. Two prostate glands present, posterior one attached to atrium by long stalk. Spermathecae (Fig. 1D, s) with very short ducts, and elongate, very thin-walled ampullae; latter about 55 μm long, about 20 μm wide, but devoid of sperm (specimen precopulatory).

Remarks. The male genitalia of *O. rallus* are virtually indistinguishable from those of *O. tannerensis* described above, but the spermathecal pores of the former are distinctly more anterior than those of the latter.

Olavius rallus is also very similar (e.g., with regard to the more anterior position of the spermathecal pores) to *O. vacuus* Erséus, 1990, a largely Caribbean species that has been found as far north as in Chesapeake Bay, Virginia (Erséus 1990). *Olavius vacuus,* however, always bears a filiform process on its pygidium and generally has a large papilla inside the wall of each copulatory sac.

Distribution and habitat.—Known only from the type locality off North Carolina, NW Atlantic. Bathyal sediments, 583 m depth.

Acknowledgments

I am indebted to Dr. J. Kudenov and Dr. Nancy Maciolek-Blake, for placing the oligochaete material at my disposal; to Ms. Barbro Löfnertz and Mrs. Birgitta Vallander, for technical assistance; and the Swedish Natural Science Research Council, for financial support.

Literature Cited

Blake, J. A., et al. 1987. Study of biological processes on the U.S. South Atlantic slope and rise. Phase 2. Report no. MMS 86-0096. U.S. Department of the Interior, Minerals Management Service, Washington, D.C. 414 pp. + appendices.

Davis, D. 1984. *Olavius cornuatus* sp. n. (Oligochaeta, Tubificidae) from Georges Bank (NW Atlantic).—Zoologica Scripta 13:273–275.

———. 1985. The Oligochaeta of Georges Bank (NW Atlantic), with descriptions of four new species.—Proceedings of the Biological Society of Washington 98:158–176.

Erséus, C. 1979a. *Inanidrilus bulbosus* gen. et sp.n., a marine tubificid (Oligochaeta) from Florida, USA.—Zoologica Scripta 8:209–210.

———. 1979b. Taxonomic revision of the marine genus *Phallodrilus* Pierantoni (Oligochaeta, Tubificidae), with descriptions of thirteen new species.—Zoologica Scripta 8:187–208.

———. 1984. Taxonomy and phylogeny of the gutless Phallordrilinae (Oligochaeta, Tubificidae), with descriptions of one new genus and twenty-two new species.—Zoologica Scripta 13:239–272.

———. 1990. The marine Tubificidae (Oligochaeta) of the barrier reef ecosystems at Carrie Bow Cay, Belize, and other parts of the Caribbean Sea, with descriptions of twenty-seven new species and revision of *Heterodrilus, Thalassodrilides* and *Smithsonidrilus*.—Zoologica Scripta 19:243–303.

Giere, O., H. Felbeck, R. Dawson, & G. Liebezeit. 1984. The gutless oligochaete *Phallodrilus leukodermatus* Giere, a tubificid of structural, ecological and physiological relevance.—Hydrobiologia 115:83–89.

Zoo-tax, Swedish Museum of Natural History, Stockholm, and (postal address): Department of Zoology, University of Göteborg, Box 25059, S-400 31 Göteborg, Sweden.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 631–639

LYCASTILLA CAVERNICOLA, A NEW FRESHWATER NEREIDID FROM AN INLAND MEXICAN CAVE (POLYCHAETA: NEREIDIDAE: NAMANEREIDINAE)

Vivianne Solís-Weiss and Luis Espinasa P.

Abstract.—A new genus and species of nereidid (*Lycastilla cavernicola*) is described from a freshwater pond within a cave found in Mexico. Its affinities with the other five genera of the subfamily are discussed with comments on the genus *Namanereis*. The new genus has more affinities with *Lycastoides* Johnson than with other genera in the subfamily despite the difference in the structure and number of tentacular cirri, and is presumably a relict species. The habitat is described and some remarks on the biology of the species are given.

In the course of a survey of a Mexican cave, a freshwater pool was found to contain a population of a previously undescribed species of Nereididae. The available material is of particular interest, not only on account of its extraordinary freshwater habitat, an elevated cave 1650 m above sea level and 176 km from the Pacific ocean, but also because it belongs to a new genus more related to *Lycastoides* than to the other genera of the subfamily that occur in freshwater and euryhaline habitats.

Study Area

The material was collected by one of us (L.E.) in the "Polychaete Pond" (after Espinasa 1989) of Isote cave (Guerrero State, Taxco de Alarcón Municipality, Mexico, 18°36′40″N, 99°33′25″W) at a distance of 176 km from the Pacific Ocean and at an altitude of 1650 m. The cave is 1567 m long and 197 m deep below ground level. The pool where the nereidids were found is 500 m from the cave entrance, at a depth of 70 m below ground level in a completely dark section of the cave. The pool is maintained by water falling from a second, smaller, more elevated pool devoid of organisms, which in turn receives its waters through percolation from the surface soil. The overflow goes to the main river at a lower level from which the pool is permanently disconnected (for a detailed description of the cave topography, see Espinasa 1989).

The pool, 80 m in length and 1–2 m in width, has a mean depth of 1–1.5 m. The cave is accessible only during the dry season (November through April). The nereidids were concentrated at a section where there was little flow (approximately 1 l/sec). The sediment was mud on the surface (about ½ cm) and sandy below.

Cave formation.—The limestone rock was formed during the lower Cretaceous period (Albian, Cenomanian and Turonian). Elevation occurred at the end of the Cretaceous (Maastrichtian) when erosion began. The presence of an igneous rock (Riolite tilzapotla) overlaying the limestone from which the water that formed the cave comes, seems to indicate that the cave was not formed until the late Oligocene (López-Ramos 1974). It is also known that the cave was already formed in the Quaternary because there is evidence (in the cave sediments) of climatic changes related to this period (Espinasa R., pers. comm.).

Thus, if the cave was formed at some point between the Oligocene and the Quaternary,

there is reason to suppose that the worms were separated from the outside communities more or less at the same period.

Materials and Methods

Sampling was done in November, during the dry season, the only period of the year when access to the cave is possible. The organisms that were seen crawling on the bottom of the pond were placed directly into a vial and fixed with 6% formalin, except for 6 of them which were placed alive into a vial with some water and sediment. After a few days in the fixative, the polychaetes were transferred to 70% alcohol. The live specimens were kept in an aquarium in the dark, occasionally adding tap water to compensate for evaporation.

Granulometric characterization of the sediment was done by sorting analysis by mesh. Organic matter content in the sediment was calculated as percent of carbon following the method of Gaudette et al. (1974).

All illustrations were made with the aid of a camera lucida attached to a stereo or a compound microscope.

The morphological terminology is derived from Hartman (1959) and Pettibone (1963).

The types are deposited in the following collections: ICML-MEX (Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mexico); USNM (Smithsonian Institution, Washington, D.C., U.S.A.); BMNH (British Museum of Natural History, London, England); AM (Australian Museum, Sydney, Australia); and HZM (Zoologisches Museum, Hamburg, Germany).

Lycastilla, new genus

Diagnosis.—Antennae, tentacular cirri and anal cirri articulate, well developed. Prostomium cleft anteriorly; with paired antennae, biarticulate palps. Tentacular segment with 3 pairs of tentacular cirri. Eversible pharynx without chitinous paragnaths or soft papillae; jaws with few teeth.

Parapodia uniramous, with neuropodial ligule only, dorsal and ventral cirri; notoaciculum and neuroaciculum present. Notoaciculum distally recurved. Setae include heterogomph spinigers and falcigers. Two anal cirri.

Etymology.—The name is a free derivation of *Lycastopsis* and *Lycastoides,* close genera, Gender: feminine.

Type species.—*Lycastilla cavernicola,* new species.

Lycastilla cavernicola, new species
Figs. 1A–E, 2A–F

Material examined.—Mexico, Guerrero State, Taxco de Alarcón municipality, Isote cavern, 18°36′40″N, 99°33′25″W.; altitude 1650 m; collected by L. Espinasa, 20 Nov 1988. (ICML POH-39001), complete with 78 setigers, 32 mm length, 1 mm width, without parapodia. 7 Paratypes (ICML POP-39001, 2; USNM 136559, 2; BMNH ZB1991.7, 1; AM W20588, 1; HZM P-20658, 1), 50–70 setigers, 24–34 mm length, 0.7–1.3 mm width.

The description is based on the holotype unless specified otherwise. Measurements were done to the closest millimeter. None were gravid.

Description.—Color in life: off-white. Dorsal blood vessel conspicuous. Color in alcohol: off-white. Prostomium quadrangular, cleft anteriorly, short, approximately ⅓ of width; deep medial groove extending from anterior margin of prostomium to middle part (Fig. 1A); without eyes; biarticulate palps shorter than frontal antennae. Antennae articulated with 5 joints (Fig. 1A). Tentacular segment shorter than following, with three pairs of tentacular cirri, articulated; posterior-medial cirri longest (Fig. 1B), extending to setiger 5, with 12 joints; jaws amber (yellow brown), each with 2 teeth (Fig. 1C).

Parapodia all uniramous, with neuropodial ligule only, similar in shape throughout

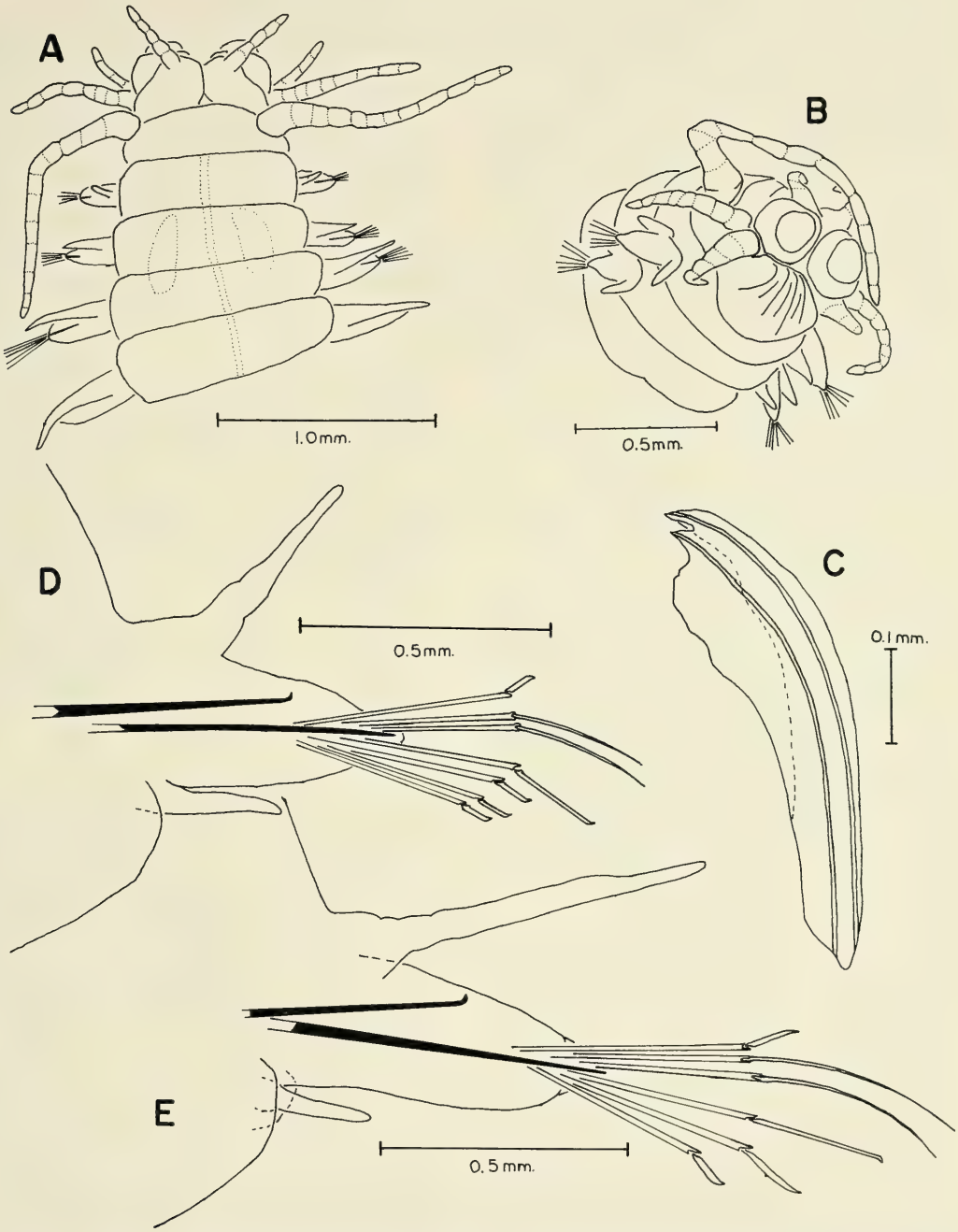


Fig. 1. *Lycastilla cavernicola*: A, Anterior end, dorsal view, dorsal longitudinal blood vessel and jaws dotted; B, Anterior end, ¾ ventral view; C, Jaw; D, Setiger 5, anterior view; E, Setiger 34, anterior view; A, C–E: holotype (ICML-POH-39-001), B: paratype (ICML-POP-39-001).

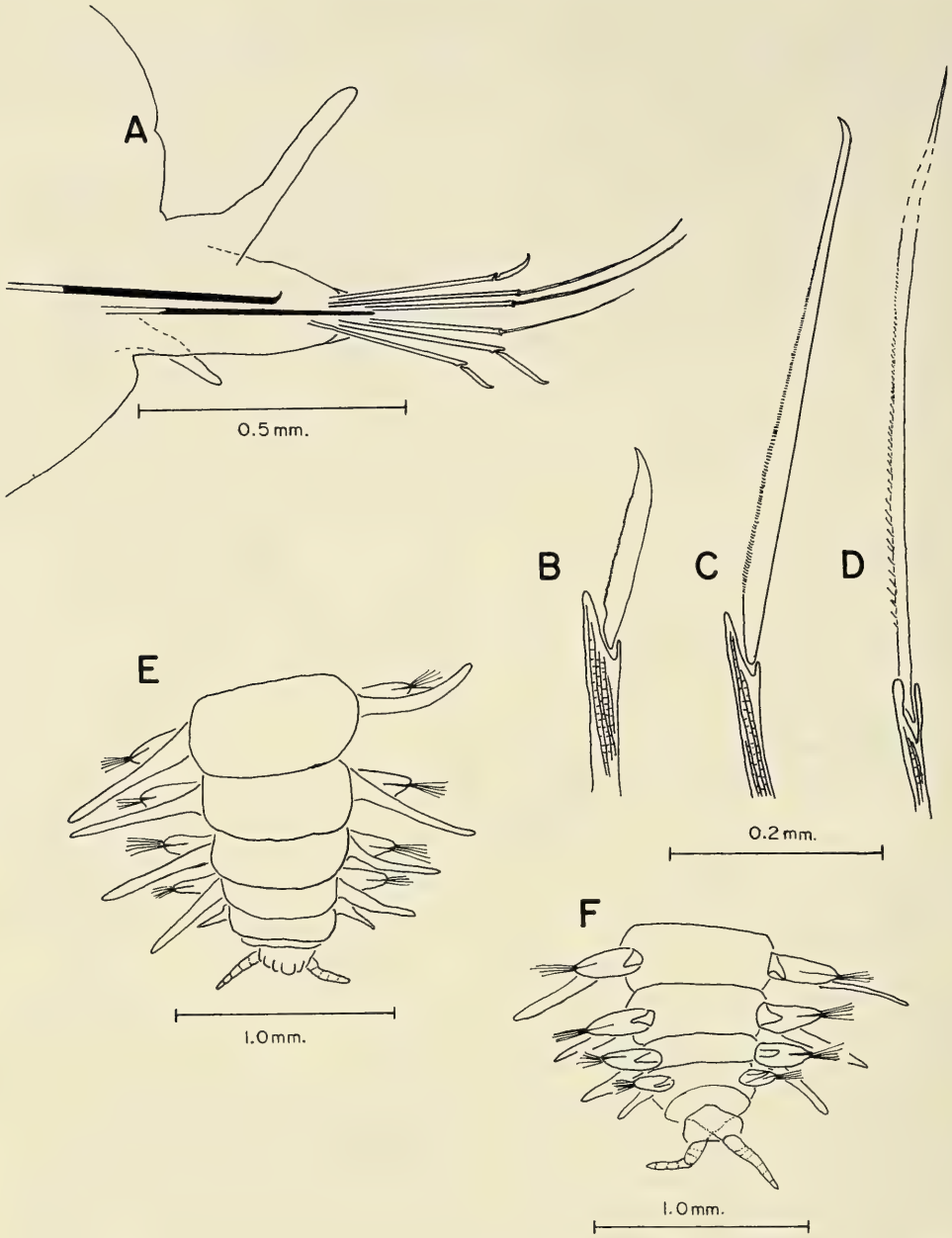


Fig. 2. *Lycastilla cavernicola*; holotype (ICML-POH-39-001) : A, Setiger 63, anterior view; B, Heterogomph falciger; C, Long bladed heterogomph pseudospiniger; D, Heterogomph spiniger; E, Posterior end, dorsal view; F, Same, ventral view.

body; first parapodium slightly smaller than following. Notopodium reduced to dorsal cirrus and notoaciculum. Dorsal cirrus digitiform, subequal in length to neuropodial ligule in anterior setigers (Fig. 1D); lengthening and surpassing neuropodial ligule slightly at midbody (Fig. 1E); decreasing in length but extending beyond neuropodial ligule posteriorly (Fig. 2A, E, F).

Pygidium terminal, with papillae. Anal

cirri ventrally produced, articulated, with ca. 5 joints, short, length equal to 2–3 posterior setigers (Fig. 2E, F).

Acicula dark brown; notoaciclulum with recurved tip, shorter than neuroaciculum.

Setae.—Dorsal neuropodium with slightly heterogomph spinigers (appear homogomph when viewed frontally) with long blades (2–3) (Fig. 2D) and with a heterogomph falciger with short rather straight blade with tapered tip (Fig. 2B, also, Fig. 1D, E).

Superior ventral neuropodium having an heterogomph falciger with long blade, the blade elongating from anterior to posterior setigers (Fig. 2C, also Fig. 1D, E; Fig. 2A), becoming spinigerous towards midbody (ca. 40th setiger). Inferior neuropodium with heterogomph falcigers showing moderate dorso ventral gradation of blade length (2–3).

Etymology.—*cavernicola* is the Latin term for cave dweller.

Discussion

Discussion of the genera and species in this subfamily is difficult because, as pointed out by Hutchings & Glasby (1985), the characters usually used to separate the nereidids at the specific level are lacking. These pertain mainly to the pharyngeal structures, complex parapodial lobes and types of notosetae present (Day 1967).

Hartman (1959), indicating that such parts are much reduced or altogether lacking in these genera, separated them as a new subfamily, the Namanereinae (sic) and used the following as generic characters: the number of pairs of tentacular cirri (three or four); the degree of middorsal cleavage of the prostomium; overall size; the number of teeth on the jaws; the relative length of the cirri; and the distribution of setae. The presence or absence of eyes was controversial.

Fitzhugh (1987), in his revision of the phylogenetic relationships within the Nereididae, recognized five genera in the subfamily Namanereidinae: *Namanereis* Chamberlin, 1919; *Cryptonereis* Gibbs, 1971; and *Lycastopsis* Augener, 1922 in one clade with *Lycastoides* Johnson, 1903 and *Namalycastis* Hartman, 1959 as a sister group. The two groups are separated by having three and four pairs of tentacular cirri respectively.

Lycastilla belongs to the first group, because of its three pairs of tentacular cirri, but has more affinities with *Lycastoides* than with the other genera as shown below in the analysis of its affinities with the other five genera.

Lycastilla is easily separated from *Cryptonereis* Gibbs, which lacks antennae, and has at maturity biramous parapodia with capillary setae (Gibbs 1971).

The main differences with *Namanereis* Chamberlin are that in *Namanereis* antennae and cirri are smooth, there is no cleft prostomium, the teeth on the jaws number from 4 to 20 (Johnson 1903), and, except in *N. kartaboensis* Treadwell, there are one to a few setae in the reduced notopodium. There are three recognized species of *Namanereis*: *N. quadraticeps* (Gay 1849), *N. kartaboensis* Treadwell, 1926 and *N. littoralis* Hutchings & Turvey, 1982. No type material appears to have been deposited for *N. quadraticeps* (Hutchings & Glasby, 1985) and the type of *N. kartaboensis* has dried (Hartman 1956). The fundamental question of the number of tentacular cirri present seems here to be controversial. When they designated the neotype of *N. quadraticeps,* Hutchings & Glasby (1985) clearly indicated in their redescription of that species, four pairs of tentacular cirri, whereas Hartman's (1959) synonymy of five species of *Lycastopsis* (*L. beumeri* Augener, 1922, *L. catarractarum* Feuerborn, 1932, *L. amboinensis* Pflugfelder, 1933, *L. hummelincki* Augener, 1933, *L. augeneri* Okuda, 1937 and *L. tecolutlensis* Rioja, 1946) with *N. quadraticeps,* as well as Fitzhugh's (1987) cladograms, indicate equally clearly three pairs. Day (1967) also remarks on the discrepancy

between Chamberlin's (1919) definition of the genus inferring 4 pairs and Hartman's definition of 3 pairs.

Hutchings & Glasby (1985) noted this difference, and, based on Fauchald's (1977) definition of the genus as having 3 *or* 4 pairs of tentacular cirri and on the fact that the notopodium is poorly developed, presume that material from southern California examined by them and identified as *N. quadraticeps* by Hartman (1968) is another species of the same genus. This is supported by the fact that there is a notoseta present in the neotype of *N. quadraticeps.* We consider, however, that the number of tentacular cirri is a character important enough to consider separating groups of genera, as did Fitzhugh (1987). In that case, if *N. quadraticeps,* as redescribed by Hutchings & Glasby, prevails, *Namanereis* should be moved to the sister group with *Lycastoides* and *Namalycastis. N. littoralis* will remain in the same genus, and *N. kartaboensis* remains problematic because the type has dried (Hartman 1956). Moreover, the material referred to *N. quadraticeps* by Hartman (1968) from California, and the material examined by Hutchings & Glasby in 1985 (from the same area, from Chile (collected by Straughan) and Ehler's material) should be moved to another genus considering they have four pairs of tentacular cirri and lack notosetae.

Lycastopsis and *Lycastilla,* on the other hand, share the following characters: three pairs of tentacular cirri, uniramous parapodia, similar small size. *Lycastopsis* differs from the new genus in having an entire (rather than a cleft) prostomium, reduced and unarticulate antennae, tentacular and anal cirri, and a straight notoaciculum. The presence of eyes is controversial: Wesenberg-Lund (1958) and Marcus (1960) considered *Lycastopsis hummelincki* Augener, 1933 as the only species of the genus lacking eyes; not recognizing that Hartman (1959) had transferred the species to the genus *Namanereis* Chamberlin, based on the presence of eyes and the jaw structure.

Its affinities with *Namalycastis* are few because besides the number of tentacular cirri (four in the latter) there are differences in the shape of the parapodial lobes (significantly enlarged at the posterior end in *Namalycastis*); the presence of eyes; no articulations in antennae and cirri (peristomial and anal); a straight notoaciculum; and the occasional presence of notosetae. Fauvel (1923) indicated that *Lycastis* (now *Namalycastis*) *brevicornis* has homogomph spinigers which would be an important difference, but it is the only species of the six genera that would have those setae reported. Rioja (1946) indicates that for *Lycastoides tecolutlensis* some superior neurosetae can easily be confused for homogomph spinigers especially if viewed frontally. This is certainly the case in *Lycastilla,* so that Fauvel's observation of this character should be taken with caution. Fitzhugh (1987), following Hartman (1959) and Gibbs (1971), indicates only heterogomph spinigers in the whole subfamily.

Lycastoides and *Lycastilla* share several characters: a cleft prostomium; articulated and well-developed antennae; tentacular and anal cirri; uniramous parapodia; distally recurved notoaciculum; eyes lacking; jaws with few teeth; and small size. *Lycastoides* differs from the new genus in having four pairs of tentacular cirri and having a greatly enlarged first basal joint of the posterior peristomial cirri (Johnson 1903). Both were collected in freshwater and elevated habitats far from the sea.

Attempts were made to collect material of *Lycastoides alticola* in the type area as indicted by Johnson (1903). A thorough exploration of the area at the altitude indicated in the literature was undertaken by one of us (L.E.) recently (Nov 1990) and no polychaetes could be found. Because the area has undergone considerable man-made changes since the first collection was done, before 1903, we conclude that it is most unlikely that this species will be found again, at least in the type area.

If we follow Hartman (1959) and Fitz-

hugh (1987), the new genus would be placed in a cladogram in the same sister group with *Cryptonereis, Lycastopsis* and the species currently assigned to *Namanereis* which have three pairs of tentacular cirri as discussed above.

Nevertheless, this genus appears to be much closer to *Lycastoides* than to the other four previously described genera, its main differences with that genus being the number of tentacular cirri and the remarkable elongation of the first joint in the peristomial cirri noted by Johnson (1903). The annulation of the antennae and cirri in only found in *Lycastilla* and *Lycastoides.*

Both *Lycastilla* and *Lycastoides* were found in strictly freshwater, rather high altitude habitats in Mexico. *Lycastoides* comes from an elevated stream (ca. 2300 m above sea level) in Sierra Laguna at the southern end of the Baja California peninsula. The state of Guerrero, where *Lycastilla* is found, borders on the Pacific ocean.

During the Cretaceous, this region was below sea level (Santiago et al. 1984). Moreover, the separation of the Gulf of California occurred about 4 million years ago (Morán Zenteno 1984). That makes it possible, considering the probable age of the cave, to have had connections between both ancestral populations. If this is the case, we can consider them as a relict, primitive fauna. Corrêa (1948) and Banse (1977) consider the Namanereidinae as more evolved than the Gymnonereidinae for example, based on the parapodial structure and considering the unirramous parapodia as an evolutionary loss. We believe that the presence of these two genera in their secluded habitats indicate that they are more primitive. Thus, as we also agree with Pettibone's (1963) comment on *Lycastopsis* as a probably relict and primitive genus, we consider the whole subfamily as the more primitive in the Nereididae.

Environmental remarks.—The maintenance of this fauna within this pool can be explained by the physical characteristics of the river. The pond is an affluent permanently disconnected from the main river that crosses the cave. The main river has a fast current that makes it impossible for silt to be deposited. The only area in the cave where there are calm waters and silt deposition is the pool containing the polychaetes. Access to the cave is impossible at other seasons of the year because of the increased river current, but the pool should not change since the river flow lies some two meters below it in the dry season.

Water temperature was 17°C measured in November 1988. The granulometric composition of the sediment was: mud (28.71%), sand (68.93%) and gravel (2.34%). The amount of organic matter present in the sediment was 1.22% of carbon (November 1988), not a very high value for marine sediments but probably high for caverns.

Biological data.—The total number of polychaetes in the pool was estimated as 2300 to 2400 organisms. Polychaetes were the largest organisms in the pool. Other organisms included copepods, trochophore larvae (about 200/ml), protozoa of at least five different species (about 10,000/ml), and bacteria (about 5×10^6/ml).

It was observed that polychaetes from the pool could be maintained in the laboratory by adding only water, thus, presumably they feed on the microfauna. The proposed food web is as follows: *L. cavernicola* feeds on bacteria, protozoa and probably their own larvae and those of copepods. Their fecal pellets in turn make up the energy source for the development of the bacteria. The presumable small amount of energy not recycled *in situ* comes from the dripping waterfall mentioned above, mainly during the rainy season. In the laboratory, we suppose that this is replaced by the small amount of light that penetrates the shaded aquarium.

Acknowledgments

We wish to thank Dr. Marian Pettibone, Professor Emeritus, (USNM), Smithsonian Institution, Washington, D.C. for kindly reviewing the manuscript and providing some

of the literature. Dr. Kristian Fauchald, Dr. Kirk Fitzhugh and J. Rolando Bastida-Zavala also provided some references for which we are thankful.

Thanks are also due to the anonymous reviewers, especially one of them for his many useful comments and suggestions which improved the manuscript.

Discussion of the manuscript and suggestions made by Dr. Christian Glasby, recognized nereidid specialist, were very helpful and are deeply acknowledged.

We also acknowledge the financial support to publish this manuscript of the Instituto de Ciencias del Mar y Limnología and its Director Dr. Jorge Carranza Fraser. This is contribution No. 700 of the I.C.M.L., U.N.A.M., Mexico.

Literature Cited

Augener, H. 1922. Ueber littoral Polychaeten von Westindien.—Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1922:38–53.

———. 1933. Susswasser Polychaeten von Bonaire.—Zoologische Jahrbucher Abteilung fur Systematik, Okologie und Geographie der Tiere 64:351–356.

Banse, K. 1977. Gymnonereidinae, new subfamily: The Nereididae (Polychaeta) with bifid parapodial neurocirri.—Journal of Natural History 11:609–628.

Chamberlin, R. V. 1919. The annelida Polychaeta.—Museum of Comparative Zoology, Harvard 48: 1–514.

Corrêa, D. 1948. A polychaete from the Amazon region.—Boletins da faculdade de Filosofía Ciências e Letras. Universidade de Saô Paulo, Zoología 13:245–257.

Day, J. H. 1967. A monograph of the Polychaeta of Southern Africa, Part 1.—British Museum of Natural History Publications, London 656:1–458.

Espinasa, R. 1989. El resumidero del Isote y la cueva de las Pozas azules.—Tepeyollotli: Gaceta de la Sociedad Mexican de Exploraciones Subterráneas 4:24–27.

Fauchald, K. 1977. The Polychaete Worms, Definitions and keys to the Orders, Families and Genera.—Natural History Museum of Los Angeles County, Science Series 28:1–190.

Fauvel, P. 1923. Polychetes errantes. Faune de France Volume 5. Kraus Reprint Nendeln, Liechtenstein (1975), 488 pp.

Feuerborn, H. J. 1932. Ein Rhizocephale und zwei Polychaeten aus dem Susswasser von Java und Sumatra.—Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie, Stuttgart. 5:618–660.

Fitzhugh, K. 1987. Phylogenetic relationships within the Nereididae (Polychaeta): implications at the subfamily level.—Bulletin of the Biological Society of Washington 7:174–183.

Gay, P. C. 1849. Annelides. Historia de Chile. Zoología Paris. 52 pp.

Gibbs, P. 1971. The polychaete fauna of the Solomon Islands.—Bulletin of the British Museum of Natural History (Zoology) 21:101–211.

Gaudette, H. E., W. R. Flight, L. Toner, & D. W. Folger. 1974. An inexpensive titration method for the determination of organic carbon in recent sediments.—Journal of Sedimentology and Petrology 44(1):249–253.

Hartman, O. 1956. Polychaetous annelids erected by Treadwell, 1891 to 1948, together with a brief chronology.—Bulletin of the American Museum of Natural History 109(2):245–310.

———. 1959. Capitellidae and Nereidae (Marine Annelids) from the Gulf side of Florida, with a review of freshwater Nereidae.— Bulletin of Marine Sciences of the Gulf and Caribbean 9(2): 153–168.

———. 1968. Atlas of errantiate Polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, 812 pp.

Hutchings, P. A., & C. J. Glasby. 1985. Additional nereidids (Polychaeta) from Eastern Australia, together with a Redescription of *Namanereis quadraticeps* (Gay) and the Synonymising of *Ceratonereis pseudoerythraensis* Hutchings & Turvey with *C. aequisetis* (Augener).—Records of the Australian Museum 37(2):101–110.

———, & S. C. Turvey. 1982. The Nereididae of South Australia.—Transactions of the Royal Society of South Australia 106(3):93–144.

Johnson, H. P. 1903. Freshwater nereids from the Pacific coast and Hawaii with remarks on freshwater Polychaeta in general.—Mark Anniversary Volume, Henry Holt & Co., New York, pp. 206–225.

López-Ramos, E. 1974. Geología de México. Third Edition. Volume 3. Secretaría de Educación Publica, Edición Escolar, México, 453 pp.

Marcus, E. du B.R. 1960. Notes on the freshwater polychaete *Lycastopsis* from Curacao.—Studies on the fauna of Curacao and other Caribbean Islands 10(46):58–63.

Morán Zenteno, D. J. 1984. Geología de la República Mexicana. Instituto Nacional de Estadística

Geografía e Informática y Facultad de Ingeniería (UNAM), México, 88 pp.

Okuda, S. 1937. Occurrence in north Japan of a new species of an aberrant polychaete genus, *Lycastopsis*.—Annotationes Zoologicae Japonenses 16(4):306–309.

Pettibone, M. 1963. Marine Polychaete Worms of the New England Region. 1. Families Aphroditidae through Trochochaetidae.—Bulletin of the United States National Museum 227:148–152.

Pflugfelder, O. 1933. Landpolychaeten aus Niederlandisch-Indien. Ergebnisse der Sunda–Expedition der Notgemeinschaft der deutschen Wissenschaft 1929-30.—Zoology Anzeiger, Leipzig 105(Heft 3/4):65–76.

Rioja, E. 1946. Estudios anelidológicos. XV. Nereidos de agua salobre de los esteros del litoral del Golfo de Mexico.—Anales del Instituto de Biología, Mexico 17:205–214.

Santiago, J. A., J. Carrillo B., & B. Martell A. 1984. Geología Petrolera de México. *In* Schlumberger Offshore Services Ed. Evaluación de formaciones en México. Ediciones especiales para Petroleos Mexicanos, 1.1–1.36.

Treadwell, A. 1926. A new polychaetous annelid from Kartobo, British Guiana, genus *Namonereis*.—Zoologica 7:101–104.

Wesenberg-Lund, E. 1958. Lesser antillean Polychaetes, chiefly from brackish water with a survey and a bibliography of fresh and brackish-water Polychaetes.—Studies on the Fauna of Curacao and other Caribbean Island 8(30):1–41.

Laboratorio de Poliquetos, Instituto de Ciencias del Mar y Limnología, U.N.A.M., Apdo Postal 70-305, Mexico, D.F. 04510, MEXICO.

PROC. BIOL. SOC. WASH.
104(3), 1991, pp. 640–646

TRIPLIGNATHIA ADRIATICA, NEW GENUS AND SPECIES, AND A TYPOLOGY OF MOUTH PARTS IN AUSTROGNATHIIDAE (GNATHOSTOMULIDA)

Wolfgang Sterrer

Abstract.–Triplignathia adriatica, a new genus and species of Gnathostomulida in the family Austrognathiidae, is described from two localities in the Adriatic (Mediterranean). Owing to the possession of three rows of jaw teeth the new genus occupies one end of a morphological cline along which the species of Austrognathiidae can be arranged; the other end is occupied by species of *Austrognatharia* with two rows of teeth one of which has only one tooth. Species of the third genus in the family, *Austrognathia,* with two full rows of teeth, lie between these extremes.

Shortly after my first encounters with the phylum Gnathostomulida (Sterrer 1965, 1966), now considered one of the most primitive living Bilateria (Ax 1986, Sterrer et al. 1986), I kept finding isolated specimens in the Adriatic of what appeared to be a species representing a new genus. I deferred describing it in the hope of collecting additional specimens or even species at other localities. Now, some 25 years later, while the number of described species of Gnathostomulida has grown to 77 in 19 genera, including 23 new species collected recently in the Pacific Ocean (Sterrer 1991a, 1991b, 1991c), no additional material pertaining to these original finds has appeared. Since the genus was mentioned in earlier systematic considerations (Sterrer 1972; "Genus XVI") it seems appropriate to name and discuss it in the context of the family.

Sediment samples were collected by diving, with a hand net or a bucket, and treated as described in detail (Sterrer 1971). A camera lucida was not used, hence specimens were not documented in as much detail as would be desirable. Furthermore, at a time when finding a single gnathostomulid specimen was considered a lucky break, I did not expect to collect several species per sample. This led me to conflate data pertaining to three species (including the one described here) into the description of the first representative of the suborder Conophoralia, *Austrognathia riedli* Sterrer, 1965. In all other respects the methods of analyzing and describing specimens and species, including measurements and indices used, are as detailed in Sterrer 1991a.

Order Bursovaginoidea Sterrer, 1972

Composition.—Two suborders, Scleroperalia Sterrer, 1972, and Conophoralia Sterrer, 1972.

Suborder Conophoralia Sterrer, 1972

Composition.—Only one family, Austrognathiidae Sterrer, 1971.

Austrognathiidae Sterrer, 1971

Composition.—Two genera, *Austrognathia* Sterrer, 1965 emend. Sterrer, 1991a; and *Austrognatharia* Sterrer, 1971 emend. Sterrer, 1991a.

Triplignathia, new genus

Diagnosis.—Austrognathiidae with three rows of jaw teeth. Basal plate with three

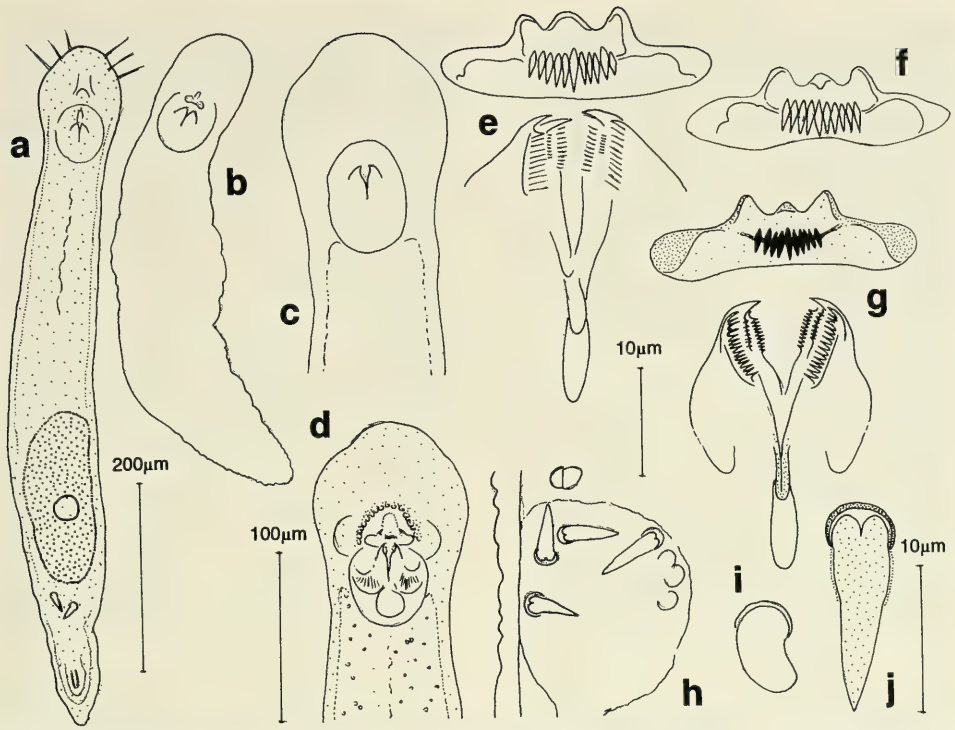


Fig. 1. *Triplignathia adriatica.* a, Adult specimen, free swimming, dorsal view; b, Juvenile specimen, slightly contracted; c and d, Rostra of two specimens; e, Basal plate and jaws, strongly squeezed; f, Basal plate of holotype; g, Basal plate and jaws, somewhat reconstructed; h, Testis; i, Bursa conulus (?); j, Conulus. Scales apply to a–b, c–d, e–g and i–j, respectively.

rostral lobes; teeth entirely contained within its outline.

Type species: *T. adriatica,* new species.

Triplignathia adriatica, new species
Figs. 1–3, Table 1

Austrognathia riedli.—Sterrer, 1965:786, fig. 3 only.

Etymology.—From the Latin *triplex* (threefold) in reference to the three rows of jaw teeth, and the type locality.

Holotype.—USNM 136897, one specimen in squeeze preparation.

Type locality.—Dubrovnik (Adriatic Sea), near Lapad, sand between Zostera at 5 m depth, 15 m from the shore; sample collected 20 Jul 1969.

Other localities.—Rovinj (Adriatic Sea), off the railway station, heterogeneous coarse sand with detritus at 3–4 m depth, April 1965 (cf. Sterrer 1965), 1 specimen; Val di Lone, fine sand at 2–3 m depth, 28 Aug 1967, 3 specimens; Isola Rossa, seaward of a shallow Posidonia patch, fine sand with detritus, 8–10 m, August 1968, 2 specimens.

Diagnosis.—Plump *Triplignathia* (index 8.13) with broad rostrum (index 0.81). Basal plate 7.83 μm long, 24.20 μm wide (index 0.33), with median lobe usually slightly smaller than lateral lobes. Jaws 21.50 μm long; dorsal row with 9.25 teeth, median row with 7.67 and ventral row with 13.00 teeth. Conuli delicate, with rounded hat, to 14 μm long and 9 μm wide (index 2.90).

Description.—Organization and behavior: Colorless-opaque. Mature specimens (Fig. 1a, b) ranged from 315 μm to 650 μm in length; the larger measured 80 μm in width at U 69.2 (body index 8.13). Rostrum broad

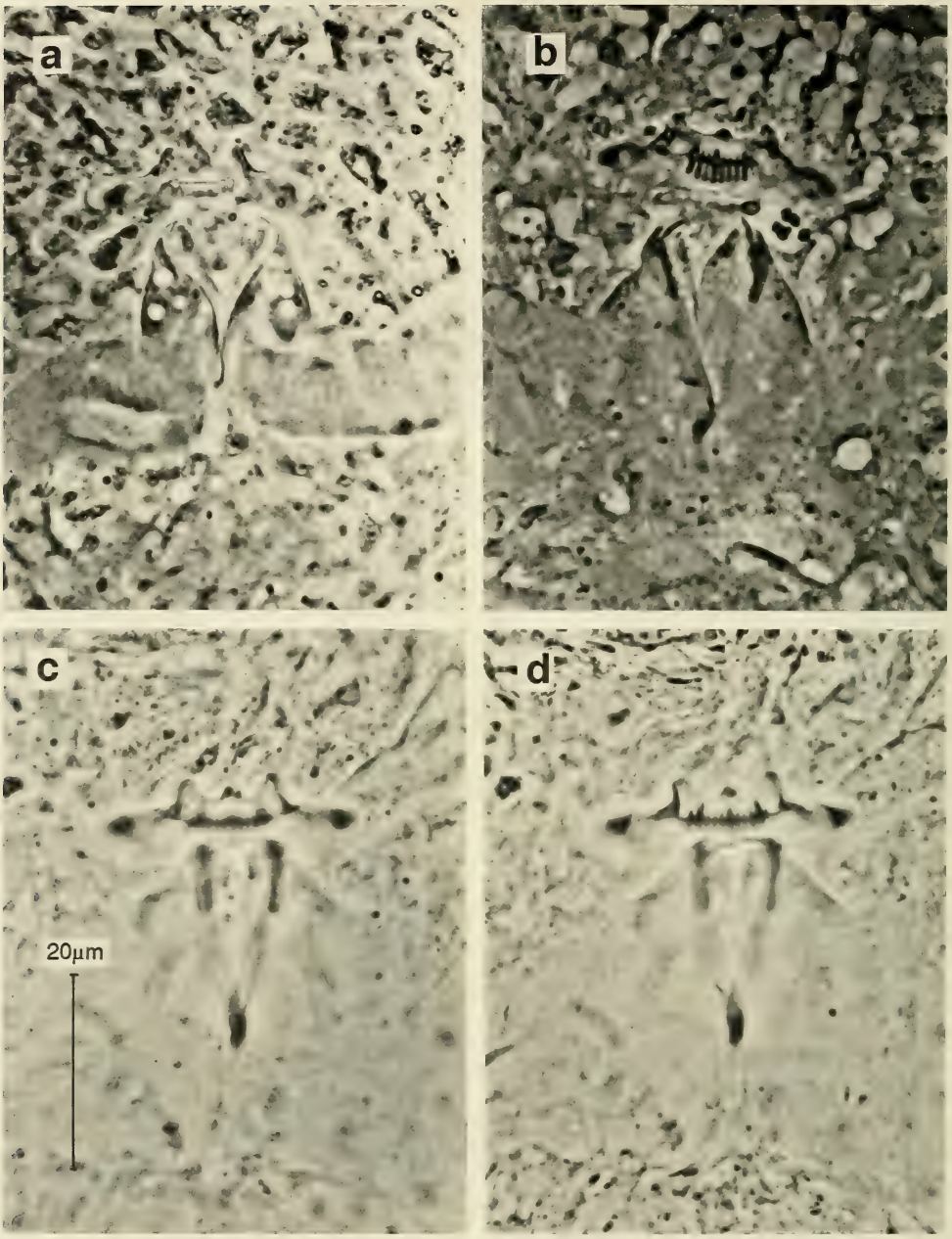


Fig. 2. *Triplignathia adriatica.* Photomicrographs of the pharynx of live specimens from Rovinj (phase contrast). a, moderately squeezed, with the median row of jaw teeth in focus; b, a more strongly squeezed specimen, with the ventral and median rows of jaw teeth in focus; c and d, a third specimen, very strongly squeezed; in c the ventral and median rows of jaw teeth are in focus, in d the dorsal row. All to the same scale.

(Fig. 1c, d), somewhat clover-shaped, 65 μm long and 80 μm wide at U 6.2 (index 0.81). Sensorium insufficiently known; consisting of at least 3 pairs of compound cilia and a pair of ciliary pits; in addition, there are long single cilia in the posterior part of the body. The tail region is also beset with rhabdoid bundles that may function as adhesive or-

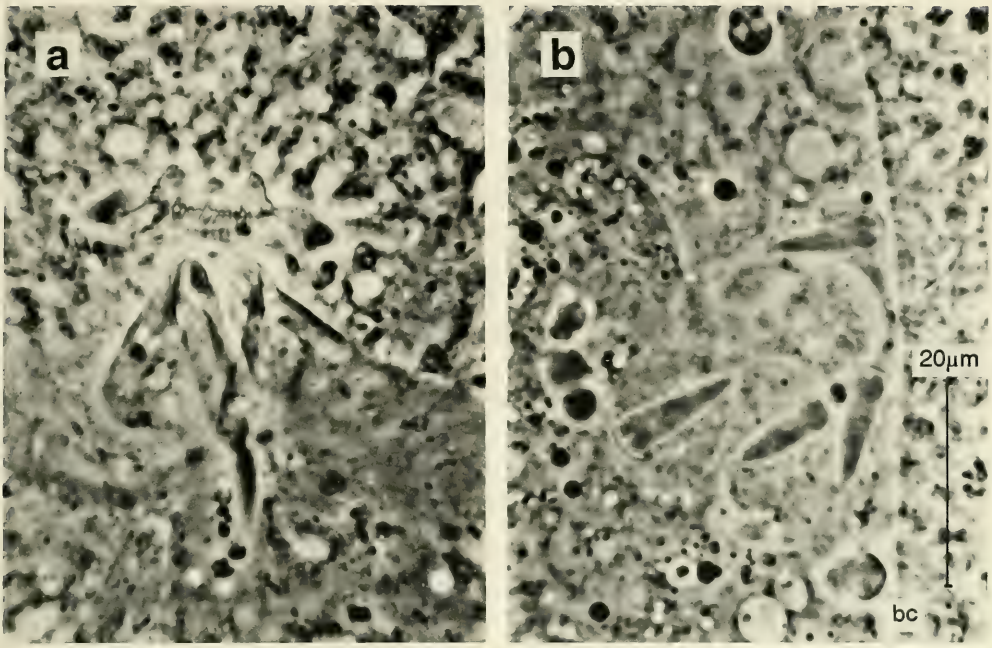


Fig. 3. *Triplignathia adriatica.* Photomicrographs of live specimens (phase contrast). a, Pharynx region of a specimen from Dubrovnik (Holotype), strongly squeezed; b, Testis with conuli, and a possible bursa conulus (bc), of a specimen from Rovinj. Both to the same scale.

gans. The animal may swim slowly but prefers to climb sluggishly over detritus particles.

Digestive tract: The oval mouth opening (Fig. 1d) leads into a spacious oral cavity which is rostrally lined by granular buccal glands, and laterally flanked by a pair of bulging prepharyngeal glands. The basal plate (Figs. 1e, f, g; 2; 3a) is 7–9 ($\bar{X}$ = 7.83) μm long and 23–26 ($\bar{X}$ = 24.20) μm wide (index 0.33). The median portion of its rostral contour is three-lobed, with the central lobe usually lower than the lateral lobes. The lateral contours of the lateral lobes form dorsally erect ridges. The caudal outline of the basal plate, probably depending on the degree of squeezing, varies from gently convex to concave. Dorsocaudally the basal plate bears 9–16 ($\bar{X}$ = 11.50) teeth of which the median tooth is longest, the rest being more or less equal. No matter how much the basal plate is squeezed, these teeth never protrude beyond the caudal outline of the basal plate. Jaws are 19–24 ($\bar{X}$ = 21.50) μm long to the symphysis, and there is a 7 μm long cauda. In addition to a strong, curved terminal tooth there are 3 rows of teeth. The ventral row, 7–8 μm long, consists of 10–18 ($\bar{X}$ = 13.00) very fine, long teeth. The median row is shorter (3 μm), and bears 7–9 ($\bar{X}$ = 7.67) short, somewhat blunter teeth. The dorsal row, about 6 μm long, bears 7–10 ($\bar{X}$ = 9.25) fairly delicate teeth.

Male system: One dorso-caudal testis, which empties into a delicate, tubular penis that lacks a tripartition. The testis contained 6 conuli in one, and 4 conuli in another specimen. Conuli (Figs. 1j; 3b) slender, 9–14 ($\bar{X}$ = 11.50) μm long and 3–5 ($\bar{X}$ = 4.00) μm wide (index 2.90), with a constriction at the rim of the hat, and another constriction further down. A faint cingulum may skirt the cone between the two constrictions. The hat is rounded but takes up only 20% of the length. The blunt end of the conulus, under the hat, appears cleft.

Female system: A mature egg may be 90 μm long. One specimen had what might be

Table 1.—*Triplignathia adriatica*: Measurements and statistics.

	Mean	*SD*	Max	Min	*n*
Body length of adults	482.50		650	315	2
Body width of adults	80.00				1
Body index of adults	8.13				1
Rostrum index of adults	0.81				1
Jaw length	21.50	2.17	24	19	6
Basal plate length	7.83	0.75	9	7	6
Basal plate width	24.20	1.30	26	23	5
Basal plate index	0.33	0.04	0.36	0.27	5
Sperm length	11.50		14	9	2
Sperm width	4.00		5	3	2
Sperm index	2.90		3.00	2.80	2

a bursa conulus (Figs. 1i; 3b) wedged between mature egg and testis: with a strong hat yet a somewhat disintegrated cone. A vagina was not observed.

Discussion.—The possession of conuli and the general organization of pharynx parts clearly identify the new species as belonging to the suborder Conophoralia. However, neither of the two existing genera can accommodate the three rows of jaw teeth, *Austrognathia* having two complete rows, and *Austrognatharia* having two rows of which the dorsal one contains only one or two teeth. In addition, the basal plate in the new species entirely surrounds its teeth, whereas in the two known genera the teeth protrude caudally beyond its contour.

A Typology of the Mouth Parts in Austrognathiidae (Fig. 4)

In an earlier paper (Sterrer 1972) I gave a preliminary definition of the genera of Austrognathiidae on the basis of mouth part anatomy. Now that we know of 3 genera (*Triplignathia, Austrognathia* and *Austrognatharia*), with a total of 17 described species (including 7 new species from the Pacific; Sterrer 1991a, 1991b, 1991c) the picture has become somewhat more complicated, making it necessary to emend (Sterrer 1991a) the diagnoses of *Austrognathia* and *Austrognatharia.* Nevertheless, the main character associations and their

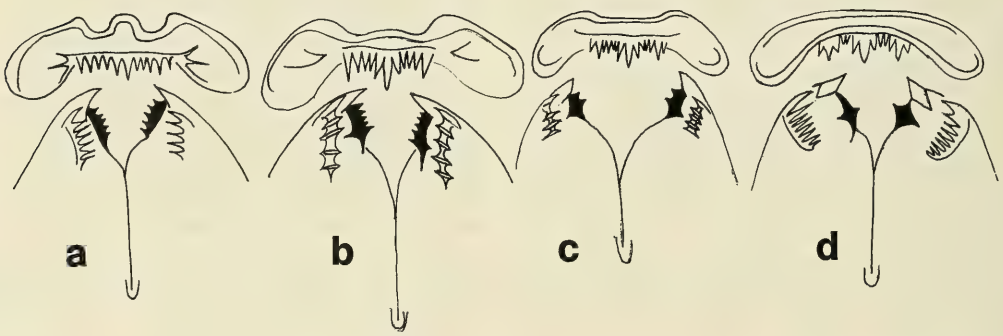


Fig. 4. Mouth part types of Austrognathiidae. a, *Austrognathia singatokae*; b, *Austrognathia novaezelandiae*; c, *Austrognatharia mooreensis*; d, *Austrognatharia pecten.* The dorsal jaw tooth row is emphasized for comparison.

sequence remain intact and emerge strengthened, if anything, by the discovery of intermediates. The known species of Austrognathiidae can thus be grouped as follows:

1. "*Adriatica* Group" (Fig. 1g) typified by *Triplignathia adriatica* new genus and species: Basal plate with prominent central and lateral lobes; basal plate teeth rather uniform in size and arrangement. Jaws with 3 rows of teeth; the dorsal row with more than 3 teeth of which none is rooted.

No other species in this group.

2. "*Singatokae* Group" (Fig. 4a) typified by *Austrognathia singatokae* Sterrer, 1991a. Basal plate with prominent, often square central lobe, and fairly prominent lateral lobes; basal plate teeth rather uniform in size and arrangement. Jaws with 2 rows of teeth; the dorsal row with 3 or more teeth none of which is rooted.

Other species in this group: *A. riedli* Sterrer, 1965; *A. hymanae* Kirsteuer, 1970; *A. microconulifera* Farris, 1977; *A. christianae* Farris, 1977.

3. "*Novaezelandiae* Group" (Fig. 4b) typified by *Austrognathia novaezelandiae* Sterrer, 1991a. Basal plate with flattened or absent central lobe, and rounded lateral lobes; basal plate teeth not uniform in size, with the central and the next-to-lateral-most stronger than the rest. Jaws with 2 rows of teeth; the dorsal row with 3 or more teeth of which the caudal-most tooth is usually rooted.

Other species in this group: *A. macroconifera* Sterrer, 1991a; *A. nannulifera* Sterrer, 1991a.

4. "*Mooreensis* Group" (Fig. 4c) typified by *Austrognatharia mooreensis* Sterrer, 1991a. Basal plate with very flattened or absent central lobe, and flattened lateral lobes; basal plate teeth regionated, with one central and two lateral groups of 3 strong teeth each, separated by 2–3 weak teeth. Jaws with 2 rows of teeth; the dorsal row with 2 (rarely 1) teeth of which the caudal-most is rooted.

Other species in this group: *A. homunculus* Sterrer, 1991a.

5. "*Pecten* Group" (Fig. 4d) typified by *Austrognatharia pecten* Sterrer, 1991a. Basal plate without a central lobe; lateral lobes very flattened or absent; basal plate teeth regionated. Jaws with 2 rows of teeth; the dorsal row with one, always rooted tooth.

Other species in this group: *A. boadeni* Sterrer, 1971; *A. kirsteueri* Sterrer, 1970; *A. strunki* Farris, 1973.

Two further species of *Austrognatharia, A. sterreri* (Kirsteuer, 1969) and *A. atraclava* Ehlers & Ehlers, 1973, cannot be assigned to any group owing to insufficient data on their cuticular mouth parts.

When the groups are considered from 1 to 5, the species of Austrognathiidae represent a morphological cline of reduction, from a condition characterized by a basal plate with 3 lobes and uniform teeth, and jaws with 3 rows of uniform teeth, to a condition characterized by a basal plate without frontal lobes and with non-uniform teeth, and jaws with 2 tooth rows of which one consists of only one tooth. Three rows of jaw teeth as well as a basal plate with prominent lateral lobes can be assumed to be the plesiomorphic condition in higher Bursovaginoidea, as is evidenced by its occurrence, as a rule, in the family's outgroup, Gnathostomulidae (with the possible exception of the insufficiently known *Corculognathia* Ehlers & Ehlers, 1973).

A preliminary analysis of conulus (sperm) morphology indicates there is no matching pattern; conulus size, shape and proportions seem uncorrelated with mouth part type. In terms of biogeography it is interesting to note that the majority of species in groups 1, 2 and 5 (the "end points" of the series) have been reported from the Atlantic Ocean and Mediterranean (the exceptions being *Austrognathia singatokae* and *Austrognatharia pecten,* both from the Pacific), whereas nearly all of the species in groups 3 and 4 (the "intermediates") come from the Pa-

cific Ocean (one exception being an undescribed species from the Mediterranean). It remains to be seen whether these morphological and global distribution patterns will hold for species yet to be discovered.

Acknowledgments

I am grateful to the staff of the Institut za biologiju mora in Rovinj and of the Bioloski Institut in Dubrovnik, in particular Prof. Tomo Gamulin, for their hospitality and help.

Literature Cited

Ax, P. 1986. The position of the Gnathostomulida and Platyhelminthes in the phylogenetic system of the Bilateria. Pp. 168–180 *in* S. Conway Morris, J. D. George, R. Gibson, & H. M. Platt, eds., The origins and relationships of lower invertebrates.—The Systematics Association Special Volume No. 28:1–397.

Ehlers, B., & U. Ehlers. 1973. Interstitielle Fauna von Galapagos. II. Gnathostomulida.–Mikrofauna des Meeresbodens 22:173–199.

Farris, R. A. 1973. On *Austrognatharia strunki* nov. spec. from the Florida Keys (Gnathostomulida).—Internationale Revue der gesamten Hydrobiologie 58:577–586.

———. 1977. Three new species of Gnathostomulida from the West Atlantic. —Internationale Revue der gesamten Hydrobiologie 62:765–796.

Kirsteuer, E. 1969. On some species of Gnathostomulida from Bimini, Bahamas.—American Museum Novitates 2356:1–21.

——— 1970. On some species of meiobenthic worms of the Class Gnathostomulida from Barbados, West Indies.—American Museum Novitates 2432:1–10.

Sterrer, W. 1965. *Gnathostomula axi* Kirsteuer und *Austrognathia* (ein weiteres Gnathostomuliden-Genus) aus der Nordadria.—Zeitschrift für Morphologie und Ökologie der Tiere 55:783–795.

———. 1966. *Gnathostomula paradoxa* Ax und Vertreter von *Pterognathia* (ein neues Gnathostomuliden-Genus) von der schwedischen Westküste.—Arkiv för Zoologi 18:405–413.

———. 1970. On some species of *Austrognatharia, Pterognathia* and *Haplognathia* nov. gen. from the North Carolina coast (Gnathostomulida).—Internationale Revue der gesamten Hydrobiologie 55:371–385.

———. 1971. On the biology of Gnathostomulida.—Vie et Milieu, Suppl. 22:493–508.

———. 1972. Systematics and evolution within the Gnathostomulida.—Systematic Zoology 21:151–173.

———. 1991a. Gnathostomulida from Fiji, Tonga and New Zealand.—Zoologica Scripta 20 (in press).

———. 1991b. Gnathostomulida from Hawaii.—Zoologica Scripta 20 (in press).

———. 1991c. Gnathostomulida from Tahiti.—Zoologica Scripta 20 (in press).

———, M. Mainitz, & R. M. Rieger. 1986. Gnathostomulida: enigmatic as ever. Pp. 181–199 *in* S. Conway Morris, J. D. George, R. Gibson, & H. M. Platt, eds., The origins and relationships of lower invertebrates.—The Systematics Association Special Volume No. 28:1–397.

Bermuda Natural History Museum, P.O. Box FL 145, Flatts FLBX, Bermuda.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

% BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD
01-938 9387

Applications published in the *Bulletin of Zoological Nomenclature*

The following applications were published on 26 March 1991 in Vol. 48, Part 1 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD.

Case No.

2750 *Epizoanthus* Gray, 1867 (Cnidaria, Anthozoa): proposed conservation.

2707 *Amphiporus* Ehrenberg, 1831 (Nemertea): proposed designation of *Planaria lactiflorea* Johnston, 1828 as the type species.

2736 *Haustator* Montfort, 1810 (Mollusca, Gastropoda): proposed conservation.

2769 *Laeocochlis* Dunker & Metzger, 1874 (Mollusca, Gastropoda): proposed conservation as the correct spelling.

2732 *Ceratites nodosus* (Cephalopoda, Ammonoidea): proposed attribution of the specific name to Schlotheim, 1813, and proposed designation of a lectotype.

2742 *Vatellus* Aubé, 1837 (Insecta, Coleoptera): proposed conservation.

2763 *Coccinella undecimnotata* Schneider, [1972] (currently *Hippodamia* (*Semiadalia*) *undecimnotata*; Insecta, Coleoptera): proposed conservation of the specific name.

2748 *Plusia falcifera* Kirby, 1837 (currently *Anagrapha falcifera*; Insecta, Lepidoptera): proposed conservation of the specific name.

2799 *Simulium* (*Nevermannia*) *juxtacrenobium* (Insecta, Diptera): a proposal that availability of the specific name be taken from the intended original description by Bass & Brockhouse, 1990.

2614 *Vipio* Latreille, 1804 (Insecta, Hymenoptera): proposed designation of *Agathis longicauda* Boheman, 1853 as the type species.

2675 *Natrix gemonensis* Laurenti, 1768 (currently *Coluber gemonensis*), *Coluber viridiflavus* Lacépède, 1789 and *Coluber helveticus* Lacépède, 1789 (currently *Natrix natrix helvetica*) (Reptilia, Serpentes): proposed conservation of the specific names.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 26 March 1991 in Vol. 84, Part 1 of the *Bulletin of Zoological Nomenclature.*

Opinion No.

1623 *Risomurex* Olsson & McGinty, 1958 (Mollusca, Gastropoda): *Ricinula deformis* Reeve, 1846 designated as the type species.

1624 *Ixodes angustus* Neumann, 1899 and *I. woodi* Bishopp, 1911 (Arachnida, Acari): specific names conserved by the replacement of the holotype of *I. angustus* by a neotype.

1625 *Thyene* Simon, 1885 (Arachnida, Araneae): given precedence over *Mithion* Simon, 1884.

1626 *Corisa verticalis* Fieber, 1851 (currently *Trichocorixa verticalis*; Insecta, Heteroptera): specific name conserved.

1627 *Saissetia* Déplanche, 1859 (Insecta, Homoptera): *Lecanium coffeae* Walker, 1852 designated as the type species.

1628 *Castiarina* Gory & Laporte, 1837 (Insecta, Coleoptera): conserved.

1629 *Helophorus brevipalpis* Bedel, 1881 (Insecta, Coleoptera): given precedence over *Helophorus creticus* Kiesenwetter, 1858.

1630 *Helophorus obscurellus* Poppius, 1907 (Insecta, Coleoptera): given precedence over *Helophorus fausti* Kuwert, 1887.

1631 *Ochthebius* Leach, 1815 (Insecta, Coleoptera): *Elophorus marinus* Paykull, 1798 designated as the type species.

1632 *Exoprosopa* Macquart, 1840 (Insecta, Diptera): *Anthrax pandora* Fabricius, 1805 confirmed as the type species.

1633 *Haplocanthosaurus* Hatcher, 1903 (Reptilia, Saurischia): conserved.

1634 *Atheris* Cope, 1862 (Reptilia, Serptentes): conserved.

PROC. BIOL. SOC. WASH.
104(3), 1991, p. 649

BIOLOGICAL SOCIETY OF WASHINGTON

118th Annual Meeting, 22 May 1991

The meeting was called to order by Leslie Knapp, President, at 1:00 PM in the Waldo Schmitt Room, National Museum of Natural History.

Mike Vecchione, Treasurer, presented his report. Income from dues in 1990 was approximately equal to that of 1989, and income from subscriptions, sales of past issues of the Proceedings and Bulletins, and page charges was substantially lower, however a number of outstanding invoices remained at the time of the report. Total income for the period of 1 May 1990–1 May 1991 was 77,272 and total expenditures were $82,018. Mike indicated that the resulting deficit of $4,746 would be more than compensated for with collection of the outstanding invoices. Finalization of the 1991 budget was delayed pending a decision by the Council on turning over address file maintenance and management of memberships and subscriptions to Allen Press or to a private accountant.

Brian Robbins, Editor, then presented his report. The four issues of Volume 103 of the *Proceedings* were published on 21 March, 28 June, 25 September, and 19 December 1991, containing a total of 90 papers and 984 pages. There has been a continued decrease in number of manuscripts submitted since the mid-1980's, and there is no current backlog.

The Index to Volumes 1–100 of the *Proceedings* (1880–1987) was published camera ready in 1990. In this regard, the following motion was passed: The Biological Society of Washington, at its annual Meeting on 22 May 1991, acknowledges, with appreciation and thanks, the monumental efforts of Phyllis Spangler, for the organization and preparation of the 100 Volume Index of the *Proceedings* published in 1990.

A motion was passed for the President to appoint an ad-hoc committee to investigate the continuing downtrend in memberships over the past several years and identify possible means to reverse it.

A motion was made and seconded that the meeting be adjourned; Les adjourned the meeting at 1:20 PM.

Respectfully submitted,
G. David Johnson
Secretary

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON" a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Apendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

Proofs.—Authors will receive first proofs and original manuscript for correction and approval. Both must be returned within 48 hours to the Editor. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, **changes in proofs ($3.00 per change or revision),** and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

CONTENTS

Morphometric differentiation among West African populations of the rodent genus *Dasymys* (Muroidea: Murinae), and its taxonomic implications
Michael D. Carleton and Christine Martinez 419

A new species of frog of the *Eleutherodactylus lacrimosus* assembly from Amazonia, South America (Amphibia: Anura: Leptodactylidae) W. Ronald Heyer and Laura M. Hardy 436

Symphurus prolatinaris, a new species of shallow-water tonguefish (Pleuronectiformes: Cynoglossidae) from the eastern Pacific
Thomas A. Munroe, Martha S. Nizinski, and M. N. Mahadeva 448

Three new species of the bentho-pelagic fish genus *Plagiogeneion* from the southern Pacific and Indian Oceans (Teleostei: Emmelichthyidae) N. V. Parin 459

Matsubarichthys inusitatus, a new genus and species of velvetfish (Scorpaeniformes: Aploactinidae) from the Great Barrier Reef Stuart G. Poss and G. David Johnson 468

Studies of Neotropical caddisflies, XLVI: The Trichoptera of the Río Moche basin, Department of La Libertad, Peru Oliver S. Flint, Jr. and Luis Reyes A. 474

An examination of the shrimp family Callianideidae (Crustacea: Decapoda: Thalassinidea)
Brian Kensley and Richard W. Heard 493

Reexamination of the type material of *Munida militaris* Henderson, 1885 (Crustacea: Decapoda: Galatheidae), with the selection of a lectotype Keiji Baba and Enrique Macpherson 538

Two similar species: *Plesionika edwardsii* (Brandt, 1851) and *Plesionika crosnieri,* new species (Crustacea: Decapoda: Pandalidae) Tin-Yam Chan and Hsiang-Ping Yu 545

Eurichocheles pindatyba, a new axiid shrimp (Crustacea: Decapoda: Thalassinidea) from Brazil
Sérgio de Almeida Rodrigues and Brian Kensley 556

A large brachyuran-like larva of the Hippidae (Crustacea: Decapoda: Anomura) from the Banda Sea, Indonesia: the largest known zoea Joel W. Martin and Bernard Ormsby 561

Crabs from the Mariana Archipelago: *Bothromaia griffini* new genus and species (Brachyura: Majidae), and remarks on *Poupinia hirsuta* Guinot (Homoloidea, Poupiniidae)
Austin B. Williams and Robert B. Moffitt 569

Two new species of *Netamelita* from the Caribbean Sea (Crustacea: Amphipoda: Gammaridea)
James Darwin Thomas and J. L. Barnard 583

Skuphonura kensleyi (Crustacea: Isopoda), a new anthuridean species from the Caribbean coast of Colombia Richard C. Brusca and Hans-Georg Müller 593

Paranebalia belizensis, a new species from shallow waters off Belize, Central America (Crustacea: Malacostraca: Leptostraca) Richard F. Modlin 603

A scanning electron microscope study of the buccal complex of *Metapeniculus antofagastensis* (Copepoda: Pennellidae) Raúl Castro Romero and Hernán Baeza Kuroki 613

Calanus euxinus, new name, a replacement name for *Calanus ponticus* Karavaev, 1894 (Copepoda: Calanoida) Kuni Hulsemann 620

Records of the marine genus *Bathydrilus* (Oligochaeta: Tubificidae) from California, with descriptions of two new species Christer Erséus 622

Two new deep-water species of the gutless genus *Olavius* (Oligochaeta: Tubificidae) from both sides of North America Christer Erséus 627

Lycastilla cavernicola, a new freshwater nereidid from an inland Mexican cave (Polychaeta: Nereididae: Namanereidinae) Vivianne Solís-Weiss and Luis Espinasa P. 631

Triplignathia adriatica, new genus and species, and a typology of mouth parts in Austrognathiidae (Gnathostomulida) Wolfgang Sterrer 640

International Commission on Zoological Nomenclature 647

Biological Society of Washington: 118th Annual Meeting 649

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY
OF
WASHINGTON

VOLUME 104 NUMBER 4
18 DECEMBER 1991
ISSN 0006-324X

THE BIOLOGICAL SOCIETY OF WASHINGTON

1990–1991

Officers

President: Leslie W. Knapp
President-elect: Storrs L. Olson
Secretary: G. David Johnson
Treasurer: Michael Vecchione

Elected Council

Roger F. Cressey, Jr.
Janet R. Gomon
Robert Hershler
Janet W. Reid
Wayne C. Starnes
Jeffery T. Williams

Custodian of Publications: Austin B. Williams

PROCEEDINGS

Editor: C. Brian Robbins

Associate Editors

Classical Languages: George C. Steyskal
Plants: David B. Lellinger
Insects: Wayne N. Mathis
Invertebrates: Jon L. Norenburg
Frank D. Ferrari
Rafael Lemaitre
Vertebrates: G. David Johnson

Membership in the Society is open to anyone who wishes to join. There are no prerequisites. Annual dues of $15.00 ($20.00 to non-USA addresses) include subscription to the *Proceedings of the Biological Society of Washington.* Library subscriptions to the *Proceedings* are: $25.00 within the U.S.A., $30.00 elsewhere.

The *Proceedings of the Biological Society of Washington* (USPS 404-750) is issued quarterly. Back issues of the *Proceedings* and the *Bulletin of the Biological Society of Washington* (issued sporadically) are available. Correspondence dealing with membership and subscriptions should be sent to The Treasurer, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Manuscripts, corrected proofs, editorial questions should be sent to the Editor, Biological Society of Washington, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Known office of publication: National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Printed for the Society by Allen Press, Inc., Lawrence, Kansas 66044

Second class postage paid at Washington, D.C., and additional mailing office.

POSTMASTER: Send address changes to PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON, National Museum of Natural History, Washington, D.C. 20560.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 651–668

PRELIMINARY PHYLOGENETIC SYSTEMATIC ANALYSIS OF THE MAJOR LINEAGES OF THE EUCESTODA (PLATYHELMINTHES: CERCOMERIA)

Daniel R. Brooks, Eric P. Hoberg, and Peter J. Weekes

Abstract.—Phylogenetic systematic analysis of the major groups of eucestodes, based on a suite of morphological characters, supports the hypothesis that pseudophyllideans are the sister-group of all other eucestodes, and nippotaeniideans are the sister-group of the lecanicephalideans, tetraphyllideans, and proteocephalideans, which occur in an unresolved trichotomy. Character data support inclusion of the Caryophyllidea within the Pseudophyllidea, as secondarily monozoic species related to cyathocephalids and spathebothriids, inclusion of the trypanorhynchs and tetrabothriideans within the Tetraphyllidea, and inclusion of the Cyclophyllidea within the Proteocephalidea. The Cyclophyllidea as a whole appears to be a monophyletic group but, with the exception of the taeniates, the relationships among its included members are highly ambiguous. The hypothesis that tapeworm phylogeny mirrors host phylogeny at the highest levels is not supported. Elasmobranchs appear to have been colonized secondarily at least once, but that colonization may have occurred so long ago that the eucestodes of extant elasmobranchs still show strong phylogenetic associations with their hosts.

One of the most fascinating and enigmatic products of evolution is the group of parasitic platyhelminths called the Eucestoda, or true tapeworms. The Eucestoda represents one of the major groups of parasitic platyhelminths, and its monophyly is supported by at least 12 anatomical and ultrastructural synapomorphies (Brooks 1989a, 1989b). A recent encyclopedic compilation of the known diversity of tapeworms (Schmidt 1986) listed more than 3800 species inhabiting vertebrates of all classes except the Agnatha. This substantial diversity in a wide range of hosts makes tapeworms excellent models for studying major patterns of evolution and coevolution. Such studies are hampered by a lack of rigorously documented phylogenetic hypotheses. Those few phylogenetic systematic reconstructions that have been attempted (Brooks 1978a, 1978b; Brooks et al. 1981; Brooks & Rasmussen 1985; Hoberg 1986, 1989; Moore & Brooks 1987; Brooks & Deardorff 1988; Weekes, in prep.) either concern restricted groups or are highly ambiguous due to poor understanding of appropriate outgroups.

It is our purpose in this study to provide a concise picture of the state of the evidence supporting the current higher-level relationships among eucestodes, point out potential problem areas, and encourage new studies in eucestode phylogenetics. We have based our study on traits used by previous workers to support their classifications, and checked by our own studies, so the database for our study is comparable to those used by previous workers. Consequently, we believe that this study is a worthwhile first step towards producing a solid phylogenetic classification of tapeworms. We think it is important to state, at the beginning, that the results of this analysis differ markedly from those presented previously for other major

groups of parasitic platyhelminths (Brooks et al. 1985a, 1985b, 1989; Bandoni & Brooks 1987a, 1987b). First, we have found relatively few characters useful for supporting relationships among groups. Second, we have found a great deal of unresolved ambiguity in the characterization of some key character complexes. Third, the eucestodes appear to be fascinating evolutionarily because they contain a number of "red herring" groups, whose placement in any phylogenetic scheme takes us boldly where no one has gone before. And fourth, the phylogenetic tree that results from this study supports some groupings that are highly inconsistent with widely used classifications of the tapeworms.

Methods

Determination of outgroups.—Phylogenetic systematic analysis requires evidence that the study group, or ingroup, is monophyletic, and one or more suitable outgroups, one of which is preferably the putative sister-group of the ingroup, and characters that serve to distinguish groups within the ingroup, based on outgroup comparisons (Wiley 1981, Wiley et al. 1991, Brooks & McLennan 1991). Extensive phylogenetic analysis has produced a highly-corroborated phylogenetic tree of the major groups of parasitic platyhelminths, which comprise the sub-phylum Cercomeria (see Brooks 1989b for a summary). Within that framework, the tapeworms comprise one of two sub-cohorts of the cohort Cestoidea (the other being the Amphilinidea). The sister-group of the Cestoidea is the cohort Gyrocotylidea, and the two cohorts form the infraclass Cestodaria. The monophyly of each group and the sister-group relationships of the gyrocotylideans, amphilinideans, and eucestodes are supported by the synapomorphies in the cladistic diagnoses listed below (an asterisk [*] indicates a character that is homoplasious within the Cercomeria).

Infraclass Cestodaria

Diagnosis: Osmoregulatory system becomes reticulate in late ontogeny; intestine lacking; posterior body invagination; copulatory stylet lost*; cercomer paedomorphic, reduced in size and at least partially invaginated; male genital pore not proximate to uterine opening; oral sucker/pharynx complex vestigial; ovary follicular; ovary bilobed; testes multiple, in two lateral bands; ten equal-sized hooks on cercomer in larvae; larval epidermis syncitial; vitelloducts syncitial; neodermis does not protrude to surface between epidermal cells; no desmosomes in the passage of the first excretory canal cells; no evidence of endoderm in embryos*; vitellogenic cells with only one kind of electron-dense vesiculated inclusions*.

Cohort Gyrocotylidea

Diagnosis: Rosette at posterior end of body; funnel connecting with rosette short; funnel narrow; antero-lateral genital notch present; body margins crenulate; body spines small over most of body, large at pharyngeal level; large body spines long and narrow; testes extending posteriorly only to level of metraterm; vitellaria encircling entire body, extending along entire body length; no nuclei in larval epidermis; no multiciliary nervous receptors; no extensions of neodermis into intercellular space between epidermis and basal lamina.

Cohort Cestoidea

Diagnosis: Male genital pore and vagina proximate; cercomer totally invaginated during ontogeny; excretory system opens posteriorly in later ontogeny; hooks on larval cercomer in two size classes (6 large and 4 small); protonephridial ducts lined with microvilli; subepidermal ciliary receptors with true photoreceptor functions lacking in larvae; protonephridia in larvae in posterior end of body; inner longitudinal muscle layer

well-developed [new character, see discussion below].

Sub-Cohort Amphilinidea

Diagnosis: Uterine pore and genital pores not proximate; male pore at posterior end; vaginal pore at posterior end; tegument of adults with irregular ridges and depressions; uterus "N"-shaped; uterine pore proximal to vestigial pharynx; inner longitudinal muscle layer weakly-developed [new character, see discussion below].

Sub-Cohort Eucestoda

Diagnosis: Body of adults polyzoic; cercomer lost during ontogeny; six hooks on larval cercomer; excretory system reticulate in early ontogeny; medullary portion of proglottids restricted; hexacanth embryo hatches from egg, is ingested in water; second larval stage a procercoid; third larval stage a plerocercoid; protein embedments in epidermis of hexacanth; tegument covered with microtriches; sperm lacking mitochondria; cerebral development paedomorphic, none seen in larvae.

Character analysis. —The above data provide evidence supporting the monophyly of the ingroup, and identifying, for use as outgroups, the sister-group of the ingroup and the sister-group of those two taxa. Relationships among various members of the ingroup are hypothesized on the basis of putative synapomorphies indicated by outgroup comparison of additional characters. As mentioned in the introduction, we based the study reported herein on traits used by previous workers to support their classifications, so the database for our study is comparable to those used by previous workers. The particular characters that we have chosen are those which we have confirmed to the best of our ability, based on our mutual experience with at least some members of all the major groups which we will discuss. The following are character argumentations for the various characters used to support the phylogenetic hypothesis discussed herein.

1. Structure of the uterus I: The plesiomorphic condition, exhibited by the gyrocotylideans, amphilinideans, monogeneans, digeneans, aspidobothriideans, and udonellideans, is a sinuous, tubular uterus that opens to the surface through a permanent pore. This *plesiomorphic* condition is characteristic of pseudophyllideans. All other eucestodes, including the nippotaeniideans, possess bilateral saccate uteri lacking permanent pores. This *apomorphic* character places the nippotaeniideans in the same clade as the other non-pseudophyllidean eucestodes, and supports the placement of the Pseudophyllidea as the sister-group of the rest of the eucestodes. Among those groups of non-pseudophyllideans in which pores are recognized (e.g., tetraphyllideans and tetrabothriideans), the pores form by an invagination of the subtegument that eventually fuses with an evagination of the uterine wall (Baylis 1926, Wardle & McLeod 1952). These slitlike or porelike modifications of the tegument (a dehiscence) allow the release of eggs with the expansion of a gravid proglottid.

2. Structure of the uterus II: Within those tapeworms having bilateral saccate uteri, a number of types of uterine structures have been reported. Nippotaeniideans, lecanicephalideans (in our sense, and including cathetocephalideans for reasons discussed below), and tetraphyllideans (in our sense, and including trypanorhynchs, tetrabothriideans, litobothriideans, and dioecotaeniideans, for reasons discussed below) possess relatively simple longitudinal saccate structures that occupy most of the middle of the proglottid. Proteocephalideans and taeniates possess a similar saccate structure with lateral diverticula. Other forms are found among cyclophyllidean taxa having retractable rostellums. The most widespread of these is a saccate structure that tends to fill

the proglottid (Matevosyan 1953). Two variants of this structure are recognizable, each of which may be derived independently (and we are assuming they are independent for the purposes of this preliminary analysis). These are the saccate uterus beginning to form and then breaking down into egg capsules and the saccate uterus becoming fibrotic and forming one or more paruterine organs. The structural homology of the remaining form of the uterus, a reticulum, is unclear although it may be derived from a saccate condition (Matevosyan 1953). Evaluation of the uterine structure has played a significant role in development of classifications for non-taeniate cyclophyllideans. Matevosyan (1953) suggested the necessity to elucidate fully patterns of uterine ontogeny in addition to providing definitions of structural relationships for the mature uterus in each group. Additionally, it is necessary to establish the homology for the origin of egg capsules (parenchymatous vs. uterine) (Bona 1955, 1975) and to clarify the relationships for the various forms of reticulate uteri that exist among a wide range of cyclophyllideans (e.g., among the Dilepididae: Kitner 1938; Bona 1957; Rybicka 1956, 1966; Spasskii 1966, 1968). We treat the condition found in nippotaeniideans, lecanicephalideans and tetraphyllideans as plesiomorphic to that found in proteocephalideans and taeniates; further, the condition found in proteocephalideans and taeniates is considered plesiomorphic to the expanded saccate condition found in non-taeniate cyclophyllideans; and finally, egg capsules and paruterine organs are considered independently derived from the expanded saccate condition.

3. Structure of the anterior holdfast in the adult: The plesiomorphic condition, exhibited by both the gyrocotylideans and amphilinideans, is a single apical suckerlike organ, which has been postulated to be a vestigial pharynx (Brooks et al. 1985a, Brooks 1989a). This structure is found in adult members of the Nippotaeniidea. Members of the Pseudophyllidea have bilaterally symmetrical, bipartite scolices (the "difossate" condition), in which the modifications for attachment consist of leaflike longitudinal flaps (bothria) and their modifications. All other eucestodes have bilaterally symmetrical, quadripartite scolices (the "tetrafossate" condition), in which the modifications for attachment consist of four suckers or four flaplike structures called bothridia. If the nippotaeniideans belong in the same clade as the tetrafossate eucestodes, and with the pseudophyllideans as their sister-group, which is indicated by their uterine structure, then the difossate condition characteristic of the pseudophyllideans is an autapomorphy for the group, and is derived from an earlier ancestor than the common ancestor of the nippotaeniideans plus the tetrafossate eucestodes. This supports an interpretation that both the difossate and tetrafossate conditions are apomorphic characters derived independently from the plesiomorphic condition of a single apical sucker. Developmental support for this interpretation includes the presence of an apical invagination (which we interpret as apical sucker anlagen) in procercoids of all eucestodes, and the presence of apical suckers in plerocercoids of nippotaeniideans, lecanicephalideans, most tetraphyllideans, and many proteocephalidean eucestodes.

4. Major modifications of the anterior holdfast: We have considered three major apomorphic modifications of the apical sucker at this level of analysis. The plesiomorphic condition, as indicated in character 3, is a simple apical sucker. That structure may be atrophied, in the form of a glandular mass characteristic of many proteocephalideans. It may be greatly enlarged, in the form of a protrusible myzorhynchus, characteristic of members of the lecanicephalidean lineage. The structure of the myzorhynchus itself may be variable (including its apparent secondary loss in *Discobothrium arrhynchum*), and this trait has been

used in characterizing genera of lecanicephalideans. Finally, the apical sucker may be modified into a structure containing hooks, called a *rostellum,* characteristic of cyclophyllideans and a few proteocephalideans. The rostellum may be retractable or not, and the shape and number of the hooks are variable. In addition, the rostellum has apparently been secondarily lost in a number of cyclophyllidean groups.

5. Major modifications of the tetrafossate condition: Tetrafossate eucestodes appear, at first glance, to come in two distinct varieties; those with four suckers and those with four flaplike structures called bothridia. We cannot use outgroup comparisons directly to determine which of the two major modifications of the tetrafossate condition might have arisen first because the sister-groups of the tetrafossate eucestodes, the Nippotaeniidea and the Pseudophyllidea, are not tetrafossate. However, developmental data are strongly suggestive. The plerocercoids of members of both groups (excluding the trypanorhynchs) have four suckers, and bothridia appear to arise as modifications of the sucker margins of plerocercoids (e.g., adult structures of *Calyptrobothrium* spp.; see Alexander 1963). On the basis of that evidence, we suggest that the plesiomorphic tetrafossate condition is one in which the scolex comprises four laterally-positioned suckers. Bothridia, arising as modifications of sucker margins, are apomorphic to suckers.

6. The structure of the margins of the bothridia: Among species of tetrafossate eucestodes having bothridia, members of the Trypanorhyncha, Onchobothriidae, and some of the Phyllobothriidae have relatively rigid bothridial margins. Other members of the Phyllobothriidae have rather flimsy bothridial margins. If the scolices of *Calyptrobothrium* spp. and relatives are indicative of the plesiomorphic bothridial nature (see e.g., Alexander 1963), it would appear that having flimsy margins is plesiomorphic. Hence, all those species having bothridia with rather rigid margins would form a monophyletic group within the tetraphyllideans, and those having flimsy margins would exhibit the plesiomorphic condition for the tetraphyllideans.

7. Paedomorphic development of the scolex: Within the group of tetraphyllideans having rather rigid bothridial margins are two groups (the Onchobothriidae and the Tetrabothriidae) which exhibit apparent paedomorphic development of the scolex. In those species, the adult form does not emerge until the plerocercoid is established in the definitive host (Hamilton & Byram 1974, Cake 1976, Hoberg 1987). In other eucestodes, the fully functional adult scolex morphology is expressed in the larval or juvenile stages found in intermediate hosts (Wardle & McLeod 1952, Riser 1956, Jarecka 1975, Avdeeva & Avdeev 1980, Jarecka & Burt 1984). Hoberg (1987, 1989) has suggested, on the basis of developmental sequences in the plerocercoid and young adults, that the tetrabothriideans have true bothridia with relatively rigid margins (see also Andersen and Lysfjord 1982) and exhibit paedomorphic scolex development (Baer 1954, Temirova & Skrjabin 1978).

8. Scolex tentacles: The Trypanorhyncha has been considered a member of the Tetraphyllidea by some, because of the uniform possession of bothridia in all species, and as a member of the Pseudophyllidea by others, because of the presence of four tentacles in both *Haplobothrium* and in the Trypanorhyncha, and because some trypanorhynchs have been described as being difossate and having pseudophyllidean-like eggs. However, those trypanorhynchs described as being difossate actually have two pairs of fused bothridia. Trypanorhynchs show X-shaped ovaries in cross section, and have bothridia with rather rigid margins. However, they do not exhibit paedomorphic scolex development. In addition, the tentacles of *Haplobothrium* do not usually persist in the adult scolex and are non-retractable; hence, we do not consider them

homologous with the tentacles of the trypanorhynchs. Therefore, we suggest that the tentacles of trypanorhynchs represent an autapomorphy for the group, rather than a synapomorphy linking them with *Haplobothrium.*

9. Scolex hooks: The members of the Onchobothriidae possess 1–2 pairs of hooks at the apical end of each bothridium. We do not have any reason to believe that they are in any way homologous with the tentacles of trypanorhynchs, the bothrial hooks of the pseudophyllidean genus *Triaenophorus,* or the rostellar hooks of certain cyclophyllideans and proteocephalideans. Consequently, we consider this trait synapomorphic for the Onchobothriidae.

10. Apical armature: Members of the genera *Silurotaenia* and *Electrotaenia* are characterized by having rows of prominent spines encircling the apical sucker. Members of the genera *Vermaia* and *Gangesia* have rows of hooks encircling the apical sucker, which functions as a non-retractable rostellum. We interpret the hooks as modified tegumental spines, and believe that these taxa represent the sister-groups of the cyclophyllideans. Within the cyclophyllideans, the taeniates have non-retractable rostellums with *Gangesia*-like hooks surrounding them. All others, including the enigmatic *Dasyurotaenia,* have retractable rostellums, suggesting that this genus be excluded from the Taeniidae (Beveridge 1984). We consider the structural relationships of the rostellum in *Gangesia* and the taeniates to be evidence that the latter are the sister-group of all other cyclophyllideans.

11. Development of the internal longitudinal muscle layer in proglottids: Pseudophyllideans are characterized by having extensive, but relatively poorly-organized, inner longitudinal muscle systems. Consequently, the extent or organization of the cortex is limited in each proglottid. This condition is similar to that found among gyrocotylideans and amphilinideans, and is hence considered plesiomorphic for eucestodes. Among other eucestodes (i.e., proteocephalideans and cyclophyllideans) there are highly distinct medullary and cortical regions of the parenchyma, the latter being relatively extensive, that are defined by the longitudinal musculature (Wardle & McLeod 1952). We consider this latter character apomorphic for the proteocephalidean plus cyclophyllidean assemblage provisionally, as it appears to occur convergently in members of other groups (e.g., in *Nippotaenia chaenogobii*), and because its condition in lecanicephalideans and tetraphyllideans is not well-documented.

As an aside, we note that gyrocotylideans and eucestodes tend be highly muscular, as indicated by difficulties in relaxing and flattening the worms for fixation, when compared with amphilinideans. Consequently, we consider a high degree of muscularity to be plesiomorphic for eucestodes and gyrocotylideans, and the condition found in amphilinideans to be a synapomorphy for that group (see diagnoses for gyrocotylideans, amphilinideans, and eucestodes, above).

12. Development of the egg and embryophore: Pseudophyllideans and trypanorhynchs, like amphilinideans and gyrocotylideans (and most other cercomerians), have "polylecithal" eggs [a large component of vitelline material forming a true shell that is quinone tanned; one embryonic membrane formed by the embryo (with the consequent lack of an embryophore); and "oviparous" development in which the embryo matures in the external (non-host) environment]. These forms additionally have operculate shells, and the hexacanth is a ciliated coracidium, with a unicellular protonephridium (except among the Trypanorhyncha) (Rybicka 1966, Freeman 1973, Burt 1987, Sakanari & Moser 1989). The remaining eucestodes possess "oligolecithal" eggs (a minimal vitelline component, and a shell formed by the embryo; two embryonic membranes; and "ovoviviparous" development in which the hexacanth matures in utero) (Jarecka 1975, Euzet &

Mokhtar-Maamouri 1976, Burt 1987). Among oligolecithal forms, ciliated coracidia and onchospheral flame cells are absent. The polylecithal condition is considered plesiomorphic, based on outgroup comparisons. However, based on other apomorphic characters linking trypanorhynchs with tetraphyllideans (particularly the form of the scolex and ovary) (see discussion), polylecithal eggs in trypanorhynchs would seem to be non-homologous with those in pseudophyllideans. This hypothesis is corroborated by the fact that trypanorhynch embryos lack the unicellular protonephridium of pseudophyllidean embryos.

13. Embryophore: Among most tetrafossate eucestodes the embryophore is nucleated and not hardened, structurally resembling a non-ciliated coracidium. In cyclophyllideans the embryophore is rigid, being formed from the inner envelope (Rybicka 1966). The rigid embryophore in all taeniate cyclophyllideans is striated, a trait unique for the group. Additionally, some non-taeniate cyclophyllideans have a cytoplasmic layer surrounding the embryophore (*Paricterotaenia, Diorchis, Hymenolepis, Moniezia*) whereas in others it is absent (*Dipylidium, Mesocestoides, Catenotaenia*). Beyond supporting the monophyly of the taeniates, the phylogenetic significance of the structure of the embryophore requires additional assessment; it may provide important information in resolving the relationships among the proteocephalideans and cyclophyllideans (Freeman 1973, Burt 1987).

14. Cysticercoid stage: A number of proteocephalideans, including corallobothriids and proteocephalids, have a cysticercoid stage intercalated between the procercoid and plerocercoid stages (Freeman 1973, Jarecka 1975). The majority of cyclophyllideans (non-taeniates) have the cysticercoid stage and no recognizable plerocercoid stage. We believe that the presence of a cysticercoid stage distinguishes a large group of suctoriates, possibly leaving only some species of *Proteocephalus* (those having an apical sucker and no cysticercoid stage) as a basal group. We are assuming that the cysticercoid stage in proteocephalideans is homologous with the cysticercoid stage in cyclophyllideans. Documenting the distribution of this trait among other sub-groups of proteocephalideans is important in resolving the basal relationships within this clade.

15. Cysticercus stage: All members of the taeniates have cysticerci or modifications thereof. We consider this to be a modification of the cysticercoid stage, based on the assumption (above) that all cysticercoids are homologous.

16. Primary lacuna: The absence of a primary lacuna appears to be plesiomorphic for eucestodes (Freeman 1973), and its presence apomorphic. However, as we will discuss later, either the presence or absence of a primary lacuna may be plesiomorphic for the cyclophyllideans (Freeman 1973) (and perhaps for nippotaeniideans; Yamaguti 1951, Demshin 1985).

17. Shape of ovary in cross section: The great majority of species of the Tetraphyllidea, including members of the Litobothriidea and Trypanorhyncha, have distinctive "X-shaped" ovaries when viewed in cross section. We consider this condition apomorphic, as it does not occur among the outgroups, or indeed among any other cercomerians, to our knowledge. It is true that not all tetraphyllideans possess X-shaped ovaries, and we will discuss the implications of that observation later.

18. Relative position of the vitellaria: Proteocephalideans (except for the Monticelliidae), most lecanicephalideans, and most tetraphyllideans have medullary vitellaria. A few pseudophyllideans have medullary vitellaria (including all of the caryophyllideans), and all eucestodes with compact vitellaria, including the Cyclophyllidea, have medullary vitellaria. The cortical condition is found in the outgroups and extensively among pseudophyllideans (it also occurs among some tetraphyllid-

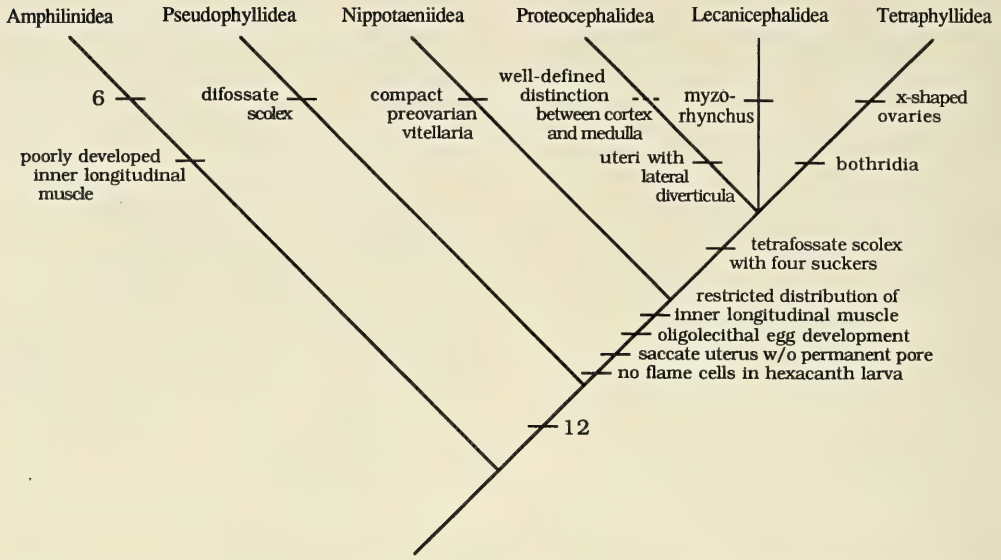


Fig. 1. Phylogenetic tree depicting five major groups of eucestodes based on the synapomorphic traits listed next to each slash mark on the tree. Numbers next to slash marks on the Amphilinidea line (sister-group) and the line uniting all eucestodes indicate number of synapomorphic traits supporting the monophyly of the groups.

eans, lecanicephalideans, and all or most of the trypanorhynchs). We consider cortical vitellaria plesiomorphic and medullary vitellaria apomorphic.

19. Distribution and structure of vitellaria: The plesiomorphic condition, exhibited by amphilinideans, some pseudophyllideans, and some tetrafossate eucestodes, is vitellaria in two cortical lateral longitudinal rows of follicles. There are several variations in vitelline structure and distribution. Most pseudophyllideans and trypanorhynchs, along with some tetraphyllideans and lecanicephalideans, exhibit circum-cortical vitellaria. Most proteocephalideans possess vitellaria in two medullary lateral longitudinal rows of follicles. The nippotaeniideans and most tetrabothriideans have single compact *preovarian* vitellaria. The members of the Cyclophyllidea have compact *postovarian* vitellaria, as do members of *Philobythos* and *Philobythoides,* which are pseudophyllideans (Campbell 1977, 1979). We consider circum-cortical vitellaria, lateral medullary vitellaria, and some instances of compact vitellaria (in the nippotaeniideans, pseudophyllideans, and tetrabothriideans) to be derived independently from lateral cortical vitellaria. The compact vitellaria of cyclophyllideans we consider derived from a lateral medullary condition, based on the relationship between proteocephalideans and cyclophyllideans, discussed below. We consider the compact vitellaria of some pseudophyllideans, the nippotaeniideans, tetrabothriideans, and cyclophyllideans all to be independently derived conditions. We also consider the circum-cortical vitellaria found in some tetrafossate eucestodes to be derived independently from the similar condition found in many pseudophyllideans.

Results and Discussion

Phylogenetic hypothesis. —Figures 1–4 depict the phylogenetic hypothesis best supported by the data described above. We recognize five major putatively monophyletic lineages within the eucestodes, based on those characters and their polarities (Fig. 1). They are characterized as follows: (1) the

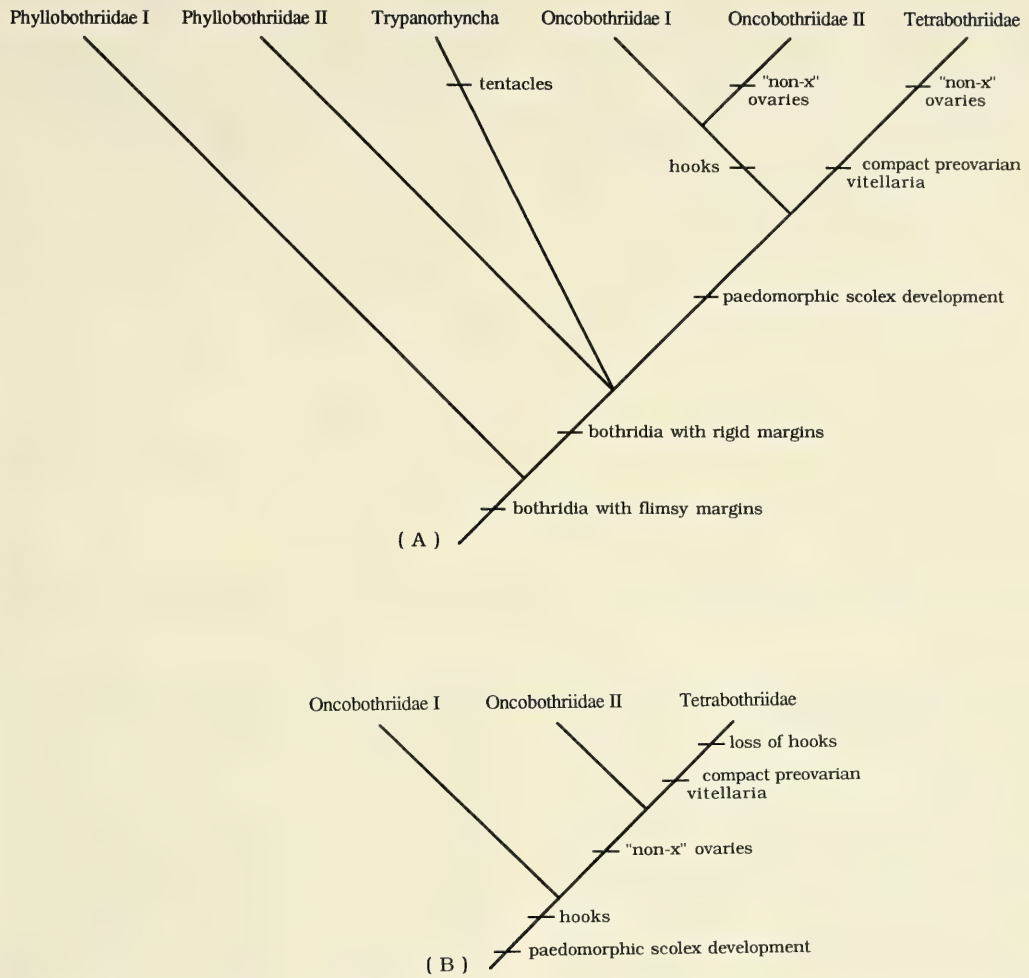


Fig. 2. (A) Phylogenetic tree depicting possible relationships among major groups of tetraphyllidean eucestodes based on the synapomorphic traits listed next to each slash mark on the tree. (B) Equally parsimonious alternative arrangement for the onchobothriids and tetrabothriideans.

Pseudophyllidea (difossate lineage), which is the sister-group of all other eucestodes; (2) the Nippotaeniidea, which is the sister-group of all other non-pseudophyllidean eucestodes; (3) the Tetraphyllidea (bothridiate lineage); (4) the Lecanicephalidea (myzorhynchoid lineage); and (5) the Proteocephalidea (proteocephalidean plus cyclophyllidean lineage). Lineages 3–5 are coordinate sister-groups and represent the tetrafossate eucestodes. The groupings depicted in Fig. 1 comprise the basic framework of eucestode relationships. Within each of these lineages are groupings of particular relevance to hypotheses of phylogenetic relationships and to evaluation of current classifications of eucestodes. Next, we will discuss some aspects of the relationships among members of each of these major groupings.

Caryophyllidea

All members of the Caryophyllidea are monozoic, and their scolex morphology is unique among eucestodes. Opinion has fluctuated between considering them to be

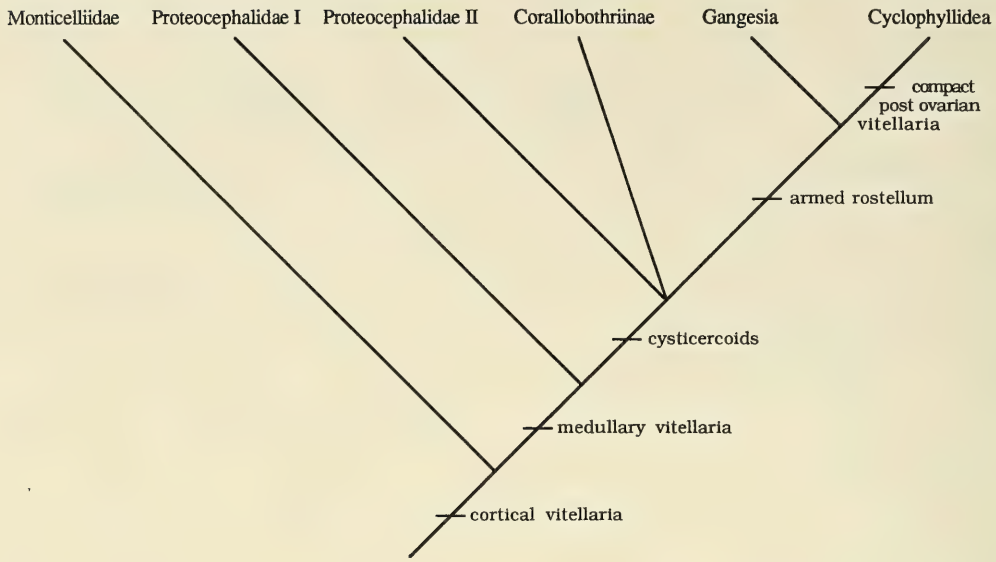


Fig. 3. Phylogenetic tree depicting relationships among members of the major groups of the proteocephalidean plus cyclophyllidean lineage based on the synapomorphic traits listed next to each slash mark on the tree.

primitively monozoic, and hence the sister-group of all other eucestodes (e.g., Llewellyn 1965; Mackiewicz 1972; Ehlers 1984, 1985a, 1985b, 1986), and considering them to be secondarily monozoic, and derived from some pseudophyllidean stock (e.g., Baer 1950, Freeman 1973), in part recognizing the relationships of the Cotyloda as defined by Wardle & Radinovsky (1974) but excluding the amphilinids and gyrocotylids, as advocated by Mackiewicz (1981). Although a full-scale phylogenetic analysis of the pseudophyllideans is beyond the scope of this study, there are clear implications about the placement of the caryophyllideans. Members of this group have non-ciliated embryos and genital pores separated by the uterine pore, two traits that appear to be apomorphic among pseudophyllideans and that place the caryophyllideans with the group of pseudophyllideans including the Spathebothriidae and Cyathocephalidae (Freeman 1973). In addition, *Cyathocephalus* and all caryophyllids share a unique feature, the utero-vaginal atrium, a common depression receiving the uterine and vaginal pores (Hart & Guberlet 1936). This placement of the caryophyllids within the pseudophyllideans, and the implication of secondary monozooy for the caryophyllids, is strengthened by the observation that the spathebothriids and cyathocephalids all exhibit inconspicuous external segmentation and apparent extreme modification or reduction of the scolex. Furthermore, Mackiewicz and Ehrenpris (1980) have shown evidence of segmentation in the arrangement of calcareous corpuscles in caryophyllids. The medullary position of the vitellaria is regarded as a secondarily derived condition in this group.

Nippotaeniidea

Most authors have recognized the primitive nature of the scolex of nippotaenideans, but have continued to link them with the relatively highly-derived Cyclophyllidea because they possess compact vitellaria (Yamaguti 1940, Hine 1977, Schmidt 1986). However, as discussed above, various members of the Pseudophyllidea and Tetraphyllidea also possess compact vitellaria, so this trait appears to be plastic among eu-

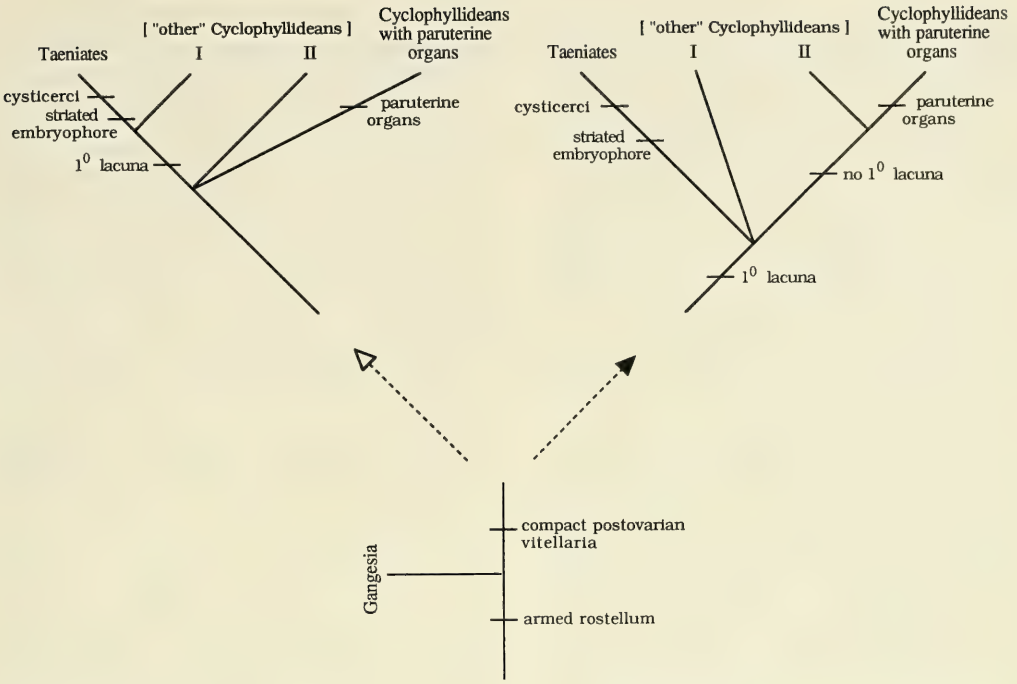


Fig. 4. Alternative phylogenetic trees depicting possible relationships of basal cyclophyllidean groups based on synapomorphic traits listed next to each slash mark on the tree.

cestodes. Furthermore, the vitellaria of nippotaeniideans are pre-ovarian, while in cyclophyllideans they are post-ovarian. We think this aspect of the vitelline structure in nippotaeniideans is synapomorphic for the group. Finally, nippotaeniids lack any of the other presumed apomorphic traits exhibited by cyclophyllideans. Consequently, the phylogenetic analysis places them in a relatively plesiomorphic position (Freeman 1973).

Majors Groups within the Tetraphyllidea

Traditionally, two major groups have been recognized within this assemblage, those having hooks on the scolex and those lacking such hooks. We believe that the first group, the Phyllobothriidae, is paraphyletic, based on differences in bothridial morphology (character 6, above and Fig. 2) and that two additional groups also belong in this assemblage, based on the characters shown in Fig. 2A, which depicts the phylogenetic relationships among these five groups based on the characters discussed above. When we take into account that the ovaries of members of *Phoreiobothrium,* and of the Tetrabothriideans, are digitiform and not X-shaped in cross section, the set of relationships shown in Fig. 2B becomes possible. If this second arrangement is consistent with the phylogenetic relationships among these tapeworms, it would imply that the ancestor of the tetrabothriideans secondarily lost its bothridial hooks. At present, we have no evidence that this might be the case, although we do have evidence among the cyclophyllideans that rostellar hooks have been lost on more than one occasion.

We include two groups, the Tetrabothriidae and the Trypanorhyncha, within the Tetraphyllidea that have rarely been placed there previously. The vast majority of tetrabothriideans have compact preovarian

vitellaria, which we consider synapomorphic for the group. These parasites of homeotherms have traditionally been placed in the Cyclophyllidea (Fuhrmann 1932, Wardle & McLeod 1952, Schmidt 1986) because members of the family inhabit birds and mammals and lack follicular vitellaria. However, the vitellarium in each proglottid is primitively pre-ovarian in tetrabothriideans (see phylogenetic analysis of tetrabothriidean genera by Hoberg 1989), rather than post-ovarian as in the cyclophyllideans. Hence, we consider the compact vitellaria of the tetrabothriideans to be an apomorphic trait for the group (albeit convergent with the nippotaeniideans). Hoberg's (1989) study also provided support for recognizing that the apical pads of onchobothriids and the auricular appendages of tetrabothriideans are homologous which would establish unequivocal relationship for these tapeworms within the group of tetraphyllideans where they are placed in Fig. 2.

The Trypanorhyncha have been variously considered closely related to the Tetraphyllidea, because they inhabit elasmobranchs (e.g., Baer 1950), or to the Pseudophyllidea, because they have polylecithal eggs and ciliated embryos (e.g., Wardle & MacLeod 1952). Additional evidence supporting the former placement includes the presence of X-shaped ovaries, the tetrafossate condition of the scolex, the presence of 4 (sometimes 2 pairs of fused) bothridia with rigid margins, and the lack of a uninucleated protonephridium in the embryo. The widespread occurrence of circum-cortical vitellaria in trypanorhynchs could be used as evidence for their inclusion either in the Pseudophyllidea or the Tetraphyllidea. Consequently, we consider the current weight of evidence to support inclusion of the trypanorhynchs within the group of tetraphyllideans having bothridia with rigid margins.

We have also included two small groups within the Tetraphyllidea to which some have accorded ordinal status. The Litobothriidea Dailey, 1969 contains three species inhabiting sharks, and which have X-shaped ovaries in cross section and scolices comprising only an apical sucker (Dailey 1969). The X-shaped ovary is an apomorphic trait while the scolex morphology is reminiscent of the plesiomorphic condition found in nippotaeniideans. If the ovarian morphology indicates relationship with other tetrafossate eucestodes inhabiting elasmobranchs, then the scolex morphology in litobothriideans may represent an apomorphic condition resulting from an extreme form of paedomorphosis, in which the larval holdfast morphology persists into adulthood. The Dioecotaeniidea Schmidt, 1986 contains two species inhabiting cownosed stingrays. They possess X-shaped ovaries and bothridia with rather rigid margins, but have been placed in their own order by virtue of the fact that both species are represented by worms that contain proglottids with only male or only female genitalia. While clearly a derived trait, having separate sexes is not unknown among eucestodes (e.g., the Dioecocestidae in the Cyclophyllidea) or among cercomerians (e.g., schistosomes among the Digenea). Furthermore, Brooks (1982) reported a detailed analysis of the scolex morphology of *Dioecotaenia,* and suggested close relationship with phyllobothriid genera including *Triloculoria, Pentaloculum* and *Zyxibothrium.*

The Lecanicephalidea

Schmidt & Beveridge (1990) recently proposed the order Cathetocephalidea to accommodate three species of tapeworms inhabiting primarily carcharhinid sharks, one in the Gulf of Mexico and two (one named) in Australian waters. The species exhibit ovaries that are bilobed rather than X-shaped in cross section and circum-cortical vitellaria. In addition, their scolices are described as ". . . lacking suckers, bothridia, or armature, transversely elongated perpendicular to the axis of the strobila. Apex of

scolex with two parallel bands of minute papillae separated by narrow, smooth, median band." (Schmidt & Beveridge 1990). One of the authors of this study (DRB) examined sagittal sections of the scolex of *Cathetocephalus thatcheri* Dailey & Overstreet, 1973. The scolex appears to be bipartite, with a cushion-like posterior portion and the glandular apical portion. Although lacking suckers and being transversely elongate rather than globular, this scolex structure is highly reminiscent of that described for other lecanicephalideans. Hence, at present we consider *Cathetocephalus* to be a member of the lecanicephalidean lineage (Fig. 1).

Major Groups within the Proteocephalidea

The monophyly of this group is supported by the presence of lateral branches and diverticula of the uterus. According to some authors, it is also supported by the well-developed distinction between the relatively large cortical and relatively restricted medullary regions of the proglottids (Wardle & McLeod 1952), which we include tentatively (see dashed line in Fig. 1) because the trait has not been documented extensively among tetraphyllidean and lecanicephalidean groups. This group includes those species assigned to both the Proteocephalidea and the Cyclophyllidea, excluding the nippotaeniideans and tetrabothrideans as already discussed.

Our assessment of the relationships among the members of this group is shown in Figs. 3–4. Freeman (1973) stated that the key to understanding cyclophyllidean evolution was understanding the proteocephalideans, especially *Proteocephalus*. We concur wholeheartedly! Our perspective differs from that of Freeman (1973) and Brooks (1978b), however. We do not think that the cyclophyllideans are paraphyletic or polyphyletic (once the tetrabothriideans have been removed). Rather, we think it is the proteocephalideans that are paraphyletic. Specifically, we think the various species currently assigned to *Proteocephalus* may be more closely related to a variety of different groups than to each other.

Figure 3 depicts the relationships among the proteocephalideans. There are several points of note. First, the group is not monophyletic if the cyclophyllideans are excluded. This means that those proteocephalideans having cysticercoids in their life cycles may be more closely related to cyclophyllideans than to other proteocephalideans. Second, the Monticelliidae, a group restricted to South American and African catfish, may not be monophyletic because the trait currently used to diagnose them, cortical vitellaria, is plesiomorphic. And third, the Proteocephalidae, made up mostly of the genus *Proteocephalus,* which itself accounts for about 40% of the nominal species in the group, appears to be a composite group much like the Phyllobothriidae in the Tetraphyllidea (Fig. 2).

Two alternative arrangements for the cyclophyllideans are shown in Fig. 4. Based on outgroup comparisons, the presence of a primary lacuna is an apomorphic trait. Among the cyclophyllideans, however, there appears to be homoplasy associated with the secondary loss of the lacuna that could affect our hypotheses of relationships markedly. If species of *Gangesia* or *Vermaia* have primary lacunae (and this is not yet known), the presence of a primary lacuna is plesiomorphic for all cyclophyllideans, and has been secondarily lost in some groups. This would tend to support an interpretation in which taeniates would be considered basal members of the Cyclophyllidea, and those species lacking primary lacunae, including the species having paruterine organs, would be considered a highly derived group. If, on the other hand, the presence of a primary lacuna is synapomorphic for some cyclophyllideans only, the cyclophyllideans with paruterine organs would be the basal group. In both cases, the rest of the cyclophyllid-

eans would comprise at least two separate groups.

We suggest that a positive approach to sorting out this problematical group would begin with studies elucidating the patterns of distribution and the structural homologies (where unclear) for the following (see discussion above as well): uterine structure, embryophore structure, primary lacunae, cysticercoids (are they homologous in proteocephalideans and cyclophyllideans?), and tegumental "hairs" on developing metacestodes. As far as the latter is concerned, plerocercoids of pseudophyllideans and trypanorhynchs, tetrathyridia of *Mesocestoides* spp: (modified cysticercoids), and cysticerci of taeniates all possess tegumental "hairs" during ontogeny. In contrast, the cysticercoids of at least some cyclophyllideans lack such hairs, having series of fibrous layers instead. The presence of such "hairs" on cysticerci and tetrathyridia may be plesiomorphic or convergent, depending on the distribution of hairs and fibrous layers among cysticercoids of proteocephalideans. If proteocephalidean cysticercoids lack tegumental hairs, it is possible that the fibrous layers represent a synapomorphy uniting at least some proteocephalideans and some cyclophyllideans into a group separate from the group including the taeniates and *Mesocestoides*. In that case, the Cyclophyllidea might turn out to be polyphyletic (in addition to the Proteocephalidea being paraphyletic), thus supporting the contentions of Freeman (1973) and Brooks (1978b). At the moment, however, this does not seem to be the best supported interpretation based on the available evidence.

Comparison with previous estimates of eucestode phylogeny.—The primary criterion used to determine tapeworm phylogeny in the past has been the presumed phylogeny of the vertebrate hosts (Fuhrmann 1928, Baer 1950, Wardle & McLeod 1952, Wardle & Radinovsky 1974, Dubinina 1980, Burt & Jarecka 1982). The following statement by Wardle & McLeod (1952:147) is typical, "On the basis of host distribution, the conclusion seems inescapable that tetrafossate tapeworms are more primitive than difossate forms, and that the most primitive of present-day tapeworms are the tetraphyllidean forms and the collared proteocephalids, which appear to be the results of divergent evolution from a common ancestral tetraphyllidean proteocephalidean stock." In this study, we use the characteristics of the worms themselves as evidence for phylogenetic relationships. Despite this difference in approach, we would like to stress the following points of agreement between our findings and those of at least some workers in the past: pseudophyllideans are the sister-group of all other eucestodes (Fuhrmann 1928, Baer 1950); caryophyllideans are secondarily monozoic (Baer 1950, Freeman 1973); nippotaeniideans are relatively primitive (Freeman 1973); trypanorhynchs are more closey related to some tetraphyllideans than to pseudophyllideans (Baer 1950); tetrabothriideans are most closely related to some tetraphyllideans [consider Baylis 1926: indeed many authors have (a) incorporated some tetrabothriideans with "tetraphyllideans" (Leiper & Atkinson 1915; see discussion in Wardle & McLeod 1952), (b) suggested possible affinities for these groups while referring them to different orders (Fuhrmann 1932, Baer 1954), or (c) provided classifications explicitly suggesting such relationships (Spasskii 1958, Temirova & Skrjabin 1978, Galkin 1987)]; tetraphyllideans, lecanicephalideans, and the proteocephalideans plus cyclophyllideans are coordinate groups (i.e., are related in a trichotomy [Freeman 1973]); proteocephalideans are the key to understanding cyclophyllideans (Freeman 1973; Brooks 1978a, 1978b); *Mesocestoides* might be relatively primitive (Perrier 1897, Voge 1967); and taeniates are a group (e.g., Ludwig 1886, Wardle & McLeod 1952, Freeman 1973, Wardle & Radinovsky 1974, Schmidt 1986).

Our findings diverge markedly from some of the conclusions drawn in the past, in par-

ticular with respect to the origin and evolution of tapeworms inhabiting elasmobranchs. Our phylogenetic tree identifies two lineages of eucestodes inhabiting primarily teleostean fishes, the Pseudophyllidea and the Nippotaeniidea, whose origins pre-date those of the Tetraphyllidea and Lecanicephalidea, which contain virtually all the tapeworm species inhabiting elasmobranchs. Consequently, we suggest that tapeworms inhabiting elasmobranchs originated from ancestors that inhabited bony fishes. If this is true, the high diversity of tapeworm species in elasmobranchs cannot be attributed solely to phylogenetic association. However, there is some evidence from phylogenetic studies that suggests a relatively long association between elasmobranchs and their tapeworms (Brooks et al. 1981, Brooks & Deardorff 1988). Hence, we would postulate, given the current database, that the colonization of elasmobranchs by tapeworms may have occurred very early in the evolution of vertebrates, so that the chondrichthyan species that were colonized were relatively basal members of that group.

There is additional phylogenetic evidence to support the idea that tapeworms arose after the divergence of chondrichthyans from the ancestor of the rest of the gnathostomous vertebrates. Brooks (1989b) noted that the basal members of the Aspidobothrea inhabit elasmobranchs, while none of the basal members of their sister-group, the Digenea, do so and suggested that this was evidence that the divergence of the stem aspidobothrean and stem digenean was coincident with the divergence of chondrichthyans from the stem of the rest of the gnathostomous vertebrates. We find a similar situation when we examine the members of the Cestodaria (sensu Brooks 1989b). The Gyrocotylidea are the sister-group of the Amphilinidea plus Eucestoda. Gyrocotylideans inhabit chimaeroid fishes, chondrichthyans that are the sister-group of the elasmobranchs. Amphilinideans inhabit bony fishes primitively (one derived species inhabits turtles as a result of a host-switch, see Bandoni & Brooks 1987a), including members of some of the more basal groups, such as sturgeons, and the two basal groups of eucestodes, according to our analysis, also inhabit bony fishes, including members of basal groups not inhabited by Amphilinideans. Consequently, the higher-level phylogeny of the cercomerians suggests that the evolutionary divergence between chondrichthyans and the rest of the gnathostomous vertebrates was associated with parasite divergence that pre-dated the origin of the true tapeworms.

One of the functions of phylogenetic systematic analysis is providing classifications that are indicative of current estimates of evolutionary history. At the same time, it is incumbent upon working systematists to maintain nomenclatorial stability, so that non-specialists will be able to use the classifications. In this regard, many phylogeneticists try to adopt classifications that conserve as many traditional names and taxonomic levels as possible within the context of consistency with phylogenetic relationships. In the case of this study, we have additional concern; our study is preliminary and deliberately cautious. Thus, we expect changes in the future, and phylogenetically based classifications may experience a period of relative instability for some time, although this does not seem to have been the case with the higher level classification of the cercomerians (compare Brooks et al. 1985a with Brooks 1989a, 1989b) or with the digeneans (compare Brooks et al. 1985b with Brooks et al. 1989). Therefore, we suggest that the phylogenetic hypothesis we present herein should be used as an index to the current state of phylogenetic systematic analysis of eucestodes, and not as a replacement for current classification.

Acknowledgments

Funding for this study was provided by operating grants from the Natural Sciences

and Engineering Council of Canada (NSERC) to DRB and EPH. We all express our appreciation to those who have stimulated and nurtured our individual interests in tapeworm systematics, especially Dr. R. Rausch, Dr. J. Mackiewicz, Dr. R. Overstreet, Dr. M. Dailey, and Dr. R. Campbell. We express our special thanks and dedicate this paper to the memory of Dr. Gerald D. Schmidt, who inspired all of us.

Literature Cited

Alexander, C. G. 1963. Tetraphyllidean and diphyllidean cestodes of New Zealand selachians.—Transactions of the Royal Society of New Zealand (Zoology) 3:117–142.

Andersen, K. I., & S. Lysfjord. 1982. The functional morphology of the scolex of two *Tetrabothrius* Rudolphi, 1819 species (Cestoda; Tetrabothriidae) from penguins.—Zeitschrift fur Parasitenkunde 67:299–307.

Avdeeva, N. V., & V. V. Avdeev. 1980. Osobennosti morfogeneza prikrepitel'nykh organov nekotorykh plerotserkoidov tsestod sbornogo roda *Scolex* (Tetraphyllidea) i problema ikh identifikatsii.—Parazitologiia 14:242–250.

Baer, J.-G. 1950. Phylogenie et cycles evolutifs des cestodes.—Revue Suisse de Zoologie 57:553–560.

———. 1954. Revision taxonomique et etude biologique des cestodes de la famille Tetrabothriidae, parasites d'Oiseaux de haute mer et de Mammiferes marins.—Memoires de Universite de Neuchatel Serie In-Quarto 1:4–122.

Bandoni, S. M., & D. R. Brooks. 1987a. Revision and phylogenetic analysis of the Amphilinidea Poche, 1922 (Platyhelminthes: Cercomeria: Cercomeromorpha).—Canadian Journal of Zoology 65:1110–1128.

———, & ———. 1987b. Revision and phylogenetic analysis of the Gyrocotylidea Poche, 1926 (Platyhelminthes: Cercomeria: Cercomeromorpha).—Canadian Journal of Zoology 65:2369–2389.

Baylis, H. A. 1926. Some tetrabothriid cestodes from whales of the genus *Balaenoptera*.—Zoological Journal of the Linnean Society 36:161–172.

Beveridge, I. 1984. *Dasyurotaenia robusta* Beddard, 1912 and *D. dasyuri* sp. nov., from carnivorous Australian marsupials.—Transactions of the Royal Society of South Australia 108:185–195.

Bona, F. V. 1955. Istologia delle capsule uterine di *Choanotaenia marchalli* (Mola, 1907) e considerazioni sul genere *Monopylidium* Fuhrmann, 1899 (Cestoda: Dilepididae).—Bollettino del Museo di Zoologia dell'Universita di Torino 5: 1–33.

———. 1957. La formazione dei gusci embionali e la morfologia dell'utero in *Paricterotaenia porosa* (Rud., 1810) quali elementi di guidizio per la validata' del gen. *Paricterotaenia* Fuhrmann, 1932 (Cestoda, Dilepididae).—Revista di Parassitologia 18:153–184.

———. 1975. Etude critique et taxonomique des Dilepididae Fuhrm., 1907 (Cestoda) parasites des Ciconiiformes. Considerations sur la specificite et la speciation.—Monitore Zoologia Italiano Monografia 1:1–750.

Brooks, D. R. 1978a. Systematic status of proteocephalid cestodes from reptiles and amphibians in North America with descriptions of three new species.—Proceedings of the Helminthological Society of Washington 45:1–28.

———. 1978b. Evolutionary history of the cestode order Proteocephalidea.—Systematic Zoology 27:312–323.

———. 1982. A simulations approach to discerning possible sister-groups of *Dioecotaenia* Schmidt, 1969 (Cestoda: Tetraphyllidea: Dioecotaeniidae).—Proceedings of the Helminthological Society of Washington 49:56–61.

———. 1989a. A summary of the database pertaining to the phylogeny of the major groups of parasitic platyhelminths, with a revised classification.—Canadian Journal of Zoology 67:714–720.

———. 1989b. The phylogeny of the Cercomeria (Platyhelminthes: Rhabdocoela) and general evolutionary principles.—Journal of Parasitology 75:606–616.

———, & T. L. Deardorff. 1988. *Rhinebothrium devaneyi* n. sp. (Eucestoda: Tetraphyllidea) and *Echinocephalus overstreeti* Deardorff and Ko, 1983 (Nematoda: Gnathostomatidae) in a thorny back ray, *Urogymnus asperrimus*, from Enewetak Atoll, with phylogenetic analysis of both species groups.—Journal of Parasitology 74:459–465.

———, & D. A. McLennan. 1991. Phylogeny, ecology and behavior: a research program in comparative biology. University of Chicago Press, Chicago, 434 pp.

———, & G. Rasmussen. 1985. Proteocephalid cestodes from Venezuelan catfish, with a new classification of the Monticelliidae.—Proceedings of the Biological Society of Washington 97:748–760.

———, M. A. Mayes, & T. B. Thorson. 1981. Systematic review of cestodes infecting freshwater stingrays (Chondrichthyes: Potamotrygonidae) including four new species from Venezuela.—Proceedings of the Helminthological Society of Washington 48:43–64.

———, R. T. O'Grady, & D. R. Glen. 1985a. The phylogeny of the Cercomeria Brooks, 1982

(Platyhelminthes).—Proceedings of the Helminthological Society of Washington 52:1–20.

———, ———, & ———. 1985b. Phylogenetic analysis of the Digenea (Platyhelminthes: Cercomeria) with comments on their adaptive radiation.—Canadian Journal of Zoology 63:411–443.

———, T. B. Thorson, & M. A. Mayes. 1981. Freshwater stingrays (Potamotrygonidae) and their helminth parasites: testing hypotheses of evolution and coevolution. Pp. 147–175 *in* V. A. Funk and D. R. Brooks, eds., Advances in cladistics: proceedings of the first meeting of the Willi Hennig Society, New York Botanical Garden, New York.

———, S. M. Bandoni, C. A. Macdonald, & R. T. O'Grady. 1989. Aspects of the phylogeny of the Trematoda Rudolphi, 1808 (Platyhelminthes: Cercomeria).—Canadian Journal of Zoology 67:2609–2624.

Burt, M. D. B. 1987. Early morphogenesis in the platyhelminths, with special reference to egg development and development of cestode larvae.—International Journal of Parasitology 17: 241–253.

———, & L. Jarecka. 1982. Phylogenetic host specificity of cestodes.—Memoires de la Museum National de l'Histoire Naturelle, Paris (serie A, Zoologie) 123:47–51.

Cake, E. W., Jr. 1976. A key to larval cestodes of shallow-water, benthic mollusks of the Northern Gulf of Mexico.—Proceedings of the Helminthological Society of Washington 43:160–171.

Campbell, R. A. 1977. A new family of pseudophyllidean cestodes from the deep-sea teleost *Acanthochaenus lutkenii* Gill, 1884.—Journal of Parasitology 63:301–305.

———. 1979. Two new genera of pseudophyllidean cestodes from deep-sea fishes.—Proceedings of the Helminthological Society of Washington 46: 74–87.

Dailey, M. D. 1969. *Litobothrium alopias* and *L. conformis,* two new cestodes representing a new order from elasmobranch fishes.—Proceedings of the Helminthological Society of Washington 36:218–224.

Demshin, N. I. 1985. Postembryonal development of the cestode *Nippotaenia mogurndae* (Nippotaeniidea, Nippotaeniidae).—Parazitologiiya 19:39–43.

Dubinina, M. N. 1980. Znachenie organov prikprepleniia v filogenii lentochnykh cherveii.—Parazitologicheskii Sbornik 29:65–83.

Ehlers, U. 1984. Phylogenetisches System der Plathelminthes.—Verhandlungen der naturwissenschaftlichen Vereins in Hamburg 27:291–294.

———. 1985a. Das phylogenetischen System der Plathelminthes. Gustav Fischer Verlag, Stuttgart.

———. 1985b. Phylogenetic relationships within the Platyhelminthes. Pp. 143–158 *in* Conway Morris, J. D. George, R. Gibson, and H. M. Platt, eds., The origins and relationships of lower invertebrates. Oxford University Press, Oxford.

———. 1986. Comments on a phylogenetic system of the Platyhelminthes.—Hydrobiologia 132:1–12.

Euzet, L., & F. Mokhtar-Maamouri. 1976. Developpement embryonaire de deux Phyllobothriidae (Cestoda: Tetraphyllidea).—Annales de Parasitologie 51:309–327.

Freeman, R. S. 1973. Ontogeny of cestodes and its bearing on their phylogeny and systematics. Pp. 481–517 *in* B. Dawes, ed., Advances in parasitology. Vol. 11. Academic Press, New York.

Fuhrmann, O. 1928. Cestoda.—Handbuch der Zoologie 2:181–416.

———. 1932. Les tenias des oiseaux.—Memoires de Universite de Neuchatel 8:1–381.

Galkin, A. K. 1987. O stanovlenii netsiklofillidnykh tsestod parazitov chaek.—Trudy Zoologicheskogo Instituta AN SSSR (Leningrad) 161:3–23.

Hamilton, K. A., & J. E. Byram. 1974. Tapeworm development: the effects of urea on a larval tetraphyllidean.—Journal of Parsitology 60:20–28.

Hart, J. F., & J. E. Guberlet. 1936. Cestoda from fishes of Puget Sound. I. Spathebothrioidea, a new superfamily.—Transactions of the American Microscopical Society 55:199–207.

Hine, P. M. 1977. New species of *Nippotaenia* and *Amurotaenia* (Cestoda: Nippotaeniidae) from New Zealand freshwater fishes.—Journal of the Royal Society of New Zealand 7:143–155.

Hoberg, E. P. 1986. Evolution and historical biogeography of a parasite-host assemblage: *Alcataenia* spp. (Cyclophyllidea: Dilepididae).—Canadian Journal of Zoology 64:2576–2589.

———. 1987. Recognition of larvae of the Tetrabothriidae (Eucestoda): implications for the origins of tapeworms in marine homeotherms.—Canadian Journal of Zoology 65:997–1000.

———. 1989. Phylogenetic relationships among genera of the Tetrabothriidae (Eucestoda).—Journal of Parasitology 75:617–626.

Jarecka, L. 1975. Ontogeny and evolution of cestodes.—Acta Parasitologica Polonica 23:93–114.

———, & M. D. B. Burt. 1984. The cercoid larvae of *Pseudanthobothrium hanseni* Baer, 1956 and *Pseudanthobothrium* sp. (Cestoda, Tetraphyllidea) from experimentally infected harpacticoid copepods.—Acta Parasitologica Polonica 29:23–26.

Kitner, K. E. 1938. Notes on the cestode parasites of English sparrows in Indiana.—Parasitology 30: 347–357.

Leiper, R. T., & E. L. Atkinson. 1915. Parasitic worms with a note on a free-living nematode.—British

Antarctic ("Terra Nova") Expedition, 1910 Natural History Report, Zoology 2:19–60.

Llewellyn, J. 1965. The evolution of parasitic platyhelminths. Pp. 47–78 *in* B. Dawes, ed., Advances in parasitology. Vol. 10. Academic Press, London.

Ludwig, H. 1886. Dr. Joannes Leunis Synopsis der Thierkunde. Ein Handbuch fur hohere Lehranstalten und fur Alle welche sich wissenschaftlich mit der Naturgeschichte der Thiere beschaftigen wollen. 3 ganzliche umgearbeitete, vermerhte Auflage. Vol. II. Hannover, 1231 pp.

Mackiewicz, J. S. 1972. Caryophyllidea (Cestoidea): a review.—Experimental Parasitology 31:417–512.

———. 1981. Caryophyllidea (Cestoidea): evolution and classification. Pp. 139–206 *in* B. Dawes, ed., Advances in parasitology. Vol. 19. Academic Press, London.

———, & M. B. Ehrenpris. 1980. Calcareous corpuscle distribution in Caryophyllid cestodes: possible evidence of cryptic segmentation.—Proceedings of the Helminthological Society of Washington 47:1–9.

Matevosyan, E. M. 1953. Revision of cestode dilepidid system. Pp. 395–400 *in* Contributions to helminthology published to commemorate the 75th birthday of K. I. Skrjabin. [English Translation, Israel Program for Scientific Translations, Jerusalem, 1966.]

Moore, J., & D. R. Brooks. 1987. Asexual reproduction in cestodes (Cyclophyllidea: Taeniidae): ecological and phylogenetic influences.—Evolution 41:882–891.

Perrier, E. 1897. Classification des cestoides.—Comptes Rendus (Paris) 86:552–554.

Riser, N. W. 1956. Early larval stages of two cestodes from elasmobranch fishes.—Proceedings of the Helminthological Society of Washington 23:120–124.

Rybicka, K. 1956. Tapeworms of birds (excl. Anseriformes) of Druzno Lake (Parasitofauna of the biocoenosis of Druzno Lake—part 4).—Acta Parasitologica Polonica 6:143–178.

———. 1966. Embryogenesis in cestodes. Pp. 107–186 *in* B. Dawes, ed., Advances in parasitology. Vol. 4. Academic Press, New York.

Sakanari, J. A., & M. Moser. 1989. Completed life cycle of the elasmobranch cestode, *Lacistorhynchus dollfusi* Beveridge and Sakanari, 1987 (Trypanorhyncha).—Journal of Parasitology 75: 806–808.

Schmidt, G. D. 1986. CRC handbook of tapeworm identification. CRC Press, Boca Raton, Florida, 688 pp.

———, & I. Beveridge. 1990. *Cathetocephalus australis* N. Sp. (Cestoidea: Cathetocephalidae), with proposal for Cathetocephalidea N. Ord.—Journal of Parasitology 76:337–339.

Spasskii, A. A. 1958. Kratkii analiz sistemy tsestod.—Ceskoslovensk Parasitologi 5:163–171.

———. 1966. On the heterogeneity of the genus *Anomotaenia* (Cestoda: Dilepididae).—Doklady Akademy Nauk SSSR 169:554–556. [English translation.]

———. 1968. Sravnitel'no-morfologicheskii i ekologo-geograficheskii analiz dilepidid roda *Anomotaenia* (Cestoda: Cyclophyllidea).—Paraziti Zhivotnykh i Rastenii 4:23–51.

Temirova, S. I., & A. S. Skrjabin. 1978. Tetrabotriaty i mezotsestoidaty lentochnye gel'minty ptits i mlekopitaiushchikh. Osnovy Tesestodologii 9.—Akademy Nauk SSSR, Moscow.

Voge, M. 1967. The post-embryonic developmental stages of cestodes. Pp. 247–297 *in* B. Dawes, ed., Advances in parasitology. Vol. 4. Academic Press, New York.

Wardle, R. A., & J. A. McLeod. 1952. The zoology of tapeworms. University of Minnesota Press, Minneapolis, 780 pp.

———, & S. Radinovsky. 1974. Advances in the zoology of tapeworms, 1950–1970. University of Minnesota Press, Minneapolis, 274 pp.

Wiley, E. O. 1981. Phylogenetics, the theory and practice of phylogenetic systematics. Wiley-Interscience, New York, 439 pp.

———, D. Siegel-Causey, D. R. Brooks, & V. A. Funk. 1991. The compleat cladist: a primer of phylogenetic procedures. University of Kansas Press, 158 pp. (in press).

Yamaguti, S. 1940. 13. Studies on the helminth fauna of Japan. Part 28. *Nippotaenia chaenogobii,* a new cestode representing a new order from freshwater fishes.—Japanese Journal of Zoology 8:285–291.

———. 1951. Early stages of the postembryonic development of *Nippotaenia chaenogobii* Yamaguti, 1939 (Cestoda).—Arbeiten aus dem Medizinische Facultat Okayama 7:335–337.

(DRB) Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1, Canada (also Research Associate, Departments of Ichthyology and Herpetology and Invertebrate Zoology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario Canada); (EPH) Biosystematic Parasitology Laboratory, USDA, ARS, BARC East #1180, Beltsville, Maryland 20705, U.S.A.; (PJW) School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 669–683

NEW HYDROBIID SNAILS (MOLLUSCA: GASTROPODA: PROSOBRANCHIA: TRUNCATELLOIDEA) FROM NORTH AMERICA

Fred G. Thompson and Robert Hershler

Abstract.—The following new species of Cochliopinae (Prosobranchia: Hydrobiidae) are described: *Aroapyrgus polius* from Mexico; *Cochliopa perforata* from Costa Rica; *Heleobops clytus* from the Dominican Republic; *H. torquatus* from Jamaica; *Lithococcus aletes* from Costa Rica; and *Littoridina microcona* from Costa Rica. In addition, the following new genera and species are described: *Mesobia pristina* from Honduras; and *Texapyrgus longleyi* from the United States (Texas).

The following new aquatic snails are described as preliminary to a generic review of the Cochliopinae[1] Tryon, 1866 (Hershler & Thompson 1991). These novelties represent major geographic range extensions for their respective genera, or they will be used as the basis for anatomical descriptions of taxonomic importance.

The new taxa are differentiated from either related genera or other congeners. While provision of anatomical data largely is limited to descriptions of the new genera, it should be noted that generic placement of the other new species was confirmed by study of soft parts when available.

Material studied is housed in the National Museum of Natural History (USNM) and Florida Museum of Natural History (UF). Shells were measured using WILD M-5 and M-7 dissecting microscopes equipped with ocular micrometers. Measurements are standard and have been converted to mm. Abbreviations are as follows: SH = shell height; SW = shell width; ApH = aperture height; ApW = aperture width; HBW = height of body whorl; WBW = width of body whorl; WH = whorls. The diameter of the apical shell whorl was measured perpendicular to the initial suture.

Family Hydrobiidae Troschel, 1857
Subfamily Cochliopinae Tryon, 1866
Aroapyrgus polius, new species
Fig. 1, Table 1

Description.—Shell medium-sized for the subfamily Cochliopinae, about 2.9–3.7 mm tall in adults; without obvious sexual dimorphism. Elongate-ovate with an obtuse apex. Width/height 52–63%; thin and transparent; smooth; teleoconch sculpture of very fine collabral striations. Periostracum gray. About 4.6–5.4 whorls in adult specimens; whorls inflated with a deeply impressed suture. Apical whorl low protruding; about

[1] The group of predominantly New World genera of Hydrobiidae united by possession of a sperm tube in the female genital tract (partly or completely separated from the glandular oviduct) and with male penis often having apocrine glands or papillae has been accorded subfamilial status by most recent workers and usually is referred to as the Littoridininae. However, the oldest available and therefore the valid name for this group is Cochliopinae Tryon, 1866. Authorship of Littoridininae has been attributed to Gray, 1857 (without complete literature citation) by several workers (Parodiz 1969:214, Golikov & Starobogatov 1975:211, Ioganzen & Starobogatov 1982:1144, Ponder & Warén 1988:297), but in Gray's works invariably he included the type species of *Littoridina* in the genus *Littorina* (Littorinidae) and we have found no evidence that he ever created a family-group name based on this hydrobiid. The earliest such name based on *Littoridina* is Littoridineae Thiele, 1928.

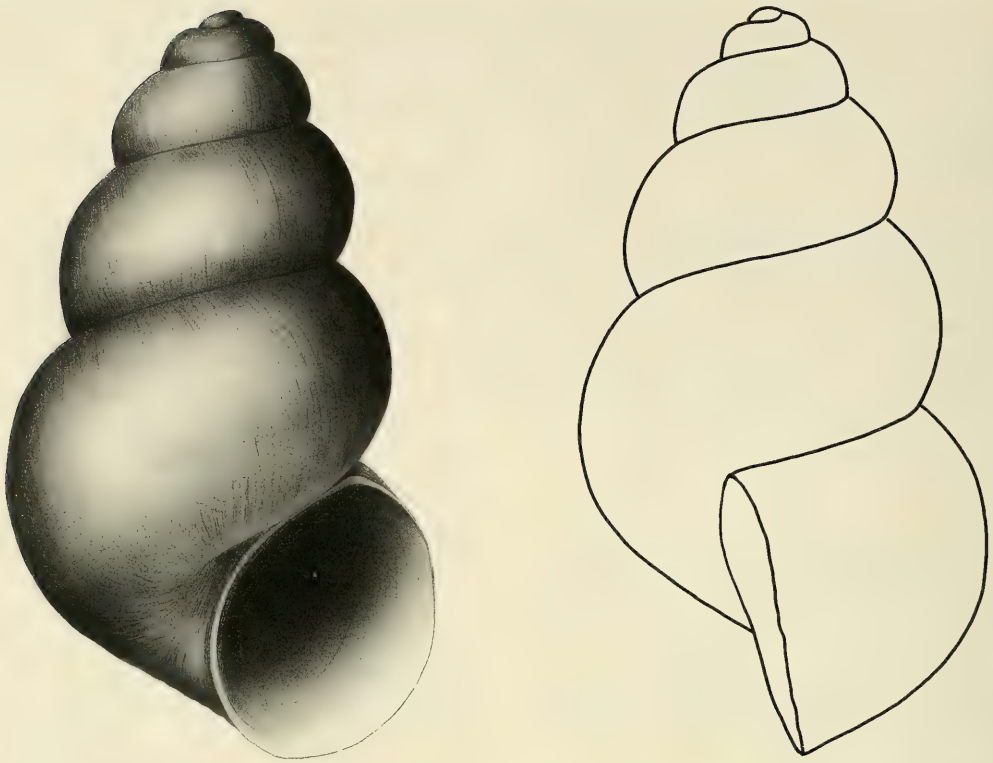


Fig. 1. *Aroapyrgus polius,* new species, holotype, UF 175028. Shell height, 3.7 mm.

0.23 mm in diameter. Umbilicus perforate; slightly obstructed by columellar lip. Aperture 37–41% of shell height; broadly ovate; width/height 80–85%; with an obtuse angle at the posterior corner. Aperture prosocline, inclined at 21–26° to coiling axis. Peristome complete across parietal margin of aperture, attached to previous whorl. Outer lip simple and thin; neither reflected nor thickened internally. Outer lip straight in lateral profile. Operculum thin, transparent, corneous; paucispiral, consisting of three rapidly expanding whorls; nucleus eccentric.

Type locality.—A small spring-fed pool 3.5 km northeast of Tamazulapan del Progreso, Oaxaca, Mexico; 2100 m elevation. Holotype: UF 175028; collected 19 Oct 1970 by Fred G. Thompson. Paratypes: UF

Table 1.—Shell parameters for *Aroapyrgus polius.* $\bar{X}$ = mean, *SD* = standard deviation.

	SH	SW	ApH	ApW	Wh	$\frac{SW}{SH}$	$\frac{ApH}{SH}$	$\frac{ApW}{ApH}$
Holotype	3.7	2.1	1.4	1.1	5.4	0.57	0.37	0.82
Paratypes, $n = 11$								
$\bar{X}$	3.2	1.9	1.3	1.1	4.9	0.59	0.39	0.83
SD	0.2	0.1	0.1	0.1	0.2	0.03	0.01	0.03
Minimum	2.9	1.8	1.2	1.0	4.6	0.52	0.37	0.80
Maximum	3.4	2.1	1.4	1.1	5.4	0.63	0.41	0.85

174989, USNM 860566, numerous specimens; same data as the holotype. The pool at the type locality was less than two meters deep with a soft silt bottom, and was congested with thick mats of *Chara.* The water was clear and had a strong odor of hydrogen sulfide. Snails were collected by washing *Chara.*

Remarks.—The genus *Aroapyrgus* includes numerous species, and is widespread from southern Ecuador and the Amazon basin of Brazil north to Veracruz, Mexico. The various species exhibit a diverse array of shell forms, varying from depressed-globose to ovate-conic. *Aroapyrgus polius* is distinguished from all other congeners by its narrow, elongate shape: shells of other congeners range from depressed-globose to ovate-conic. No close affinities within the genus are apparent at present.

Etymology.—The species name *polius* is from the Classical Greek *polios,* meaning ashy gray, and refers to the shell color.

Cochliopa perforata, new species
Fig. 2, Table 2

Description.—Shell thick; periostracum yellow-green; columellar margin of aperture opaque white. Large, 3.5–4.3 mm tall; depressed-ovate; width/height, 79–95%; body whorl width 73–86% of height. Spire very low, broadly conical. Whorls 4.2–5.1; suture weakly impressed; apical whorl 0.12–0.15 mm in diameter. Umbilicus perforate; base of last whorl with a blunt, low spiral crest around the umbilical region; crest may be obsolete except near the peristome. Sculpture consisting of fine collabral striations over most of shell; circum-umbilical region within spiral crest having a few weak raised spiral lirae that may be broken into spiral series of small papillae. Aperture strongly prosocline, inclined 38–42° to coiling axis. Aperture 60–79% of shell height, and 65–81% of body whorl height. Aperture ovate; posterior corner angular and sulcate. Peristome complete across parietal wall at maturity; parietal callus thick, opaque; outer lip thin, sharp; columellar margin thick, rounded.

Fig. 2. *Cochliopa perforata,* new species, holotype, UF 175911. Shell height, 4.1 mm.

Type locality.—A small stream 1 km northwest of the Bay of Golfito, Puntarenas Province, Costa Rica. Holotype: UF 175911; collected 27 Jul 1964 by Fred G. Thompson. Paratypes: UF 38504, USNM 850565, numerous specimens; same data as the holotype. The stream was about 5 m wide and up to one meter deep, with clear water and a gravel bottom. *Cochliopa perforata* was common, but patchy, on grass roots along the shore of the stream. It was

Table 2.—Shell parameters for *Cochliopa perforata*. $\bar{X}$ = mean, *SD* = standard deviation.

	SH	HBW	SW	ApH	ApW	Wh	$\frac{SW}{SH}$	$\frac{WBW}{HBW}$	$\frac{ApH}{SH}$
Holotype	4.1	3.7	4.5	2.5	2.4	4.25	0.91	0.81	0.61
Paratypes, $n = 12$									
$\bar{X}$	3.9	3.6	4.5	2.6	2.4	4.9	0.86	0.79	0.67
SD	0.3	0.3	0.1	0.2	0.1	0.1	0.1	0.1	0.1
Minimum	3.5	3.3	4.2	2.4	2.3	4.7	0.79	0.73	0.60
Maximum	4.3	4.0	4.7	2.9	2.5	5.1	0.95	0.86	0.79

found only within 200 m of the mouth of the stream above the bay.

Distribution.—Known only from small streams near Golfito, Puntarenas Province, Costa Rica. We have examined other specimens from the following localities: stream 7.5 km northeast of Golfito (UF 38607); small stream at northeast corner of bay, Golfito (UF 38589).

Remarks.—*Cochliopa* includes four described species (Hershler & Thompson 1991). All but *C. perforata* occur in Panama. The latter is distinct because of its large size, low spiral crest on the base of the last whorl, perforate umbilicus, and spiral threads in the circum-umbilical region. Other described species are smaller, imperforate or only narrowly rimate, lack a basal crest, and lack spiral sculpture.

Etymology.—The species name *perforata* is derived from the Latin *perforare,* to bore through, and refers to the umbilical opening.

Heleobops clytus, new species
Fig. 3, Table 3

Description.—Shell conical in shape; width/height, 49–58%. Sexually dimorphic in size; females about 3.2–4.2 mm long and with 5.1–6.0 whorls; males about 2.7–2.9 mm long and with 3.7–4.2 whorls. Suture very weakly impressed. Spire straight-sided or weakly concave in outline. Apical whorl protruding, 0.23–0.24 mm in diameter. Shell translucent, light gray. Sculpture of fine collabral striations and sparce, very fine spiral striations. Umbilicus imperforate. Aperture width/height, 69–83%; height 40–46% of shell height. Prosocline, apertural plane inclined about 20° to coiling axis. Peristome incomplete across parietal margin; outer lip arched forward slightly when viewed in lateral profile.

Type locality.—Spring 2 km east-southeast of Duverge, Independencia Province, Dominican Republic. Holotype: UF 175170; collected 6 Feb 1976 by Fred G. Thompson and Beverly E. Johnson. Paratypes: UF 135428, USNM 860564, numerous specimens; same data as the holotype. The type locality is a small seepage spring run about one meter wide and less than 0.5 m deep. Snails were collected by washing mats of filamentous algae.

Distribution.—The species is common in the Lago de Enriquillo drainage. We have examined specimens from the following localities. Dominican Republic. Independencia Province: spring 5.0 km west-northwest of Duverge (UF 174881); spring 6.0 km west-northwest of Duverge (UF 174884); spring 1.0 km west of Las Baitoas (UF 174887); spring, Boca de Cachon (UF 174891); spring along north shore of Lago de Enriquillo, 4.0 km east of La Descubierta (UF 174894); spring 4.0 km east-northeast of Neiba (UF 174896).

Remarks.—This species is very similar in appearance to *Heleobops docimus* Thompson, 1968 from Florida. Its shell differs from the latter by having a slightly less impressed

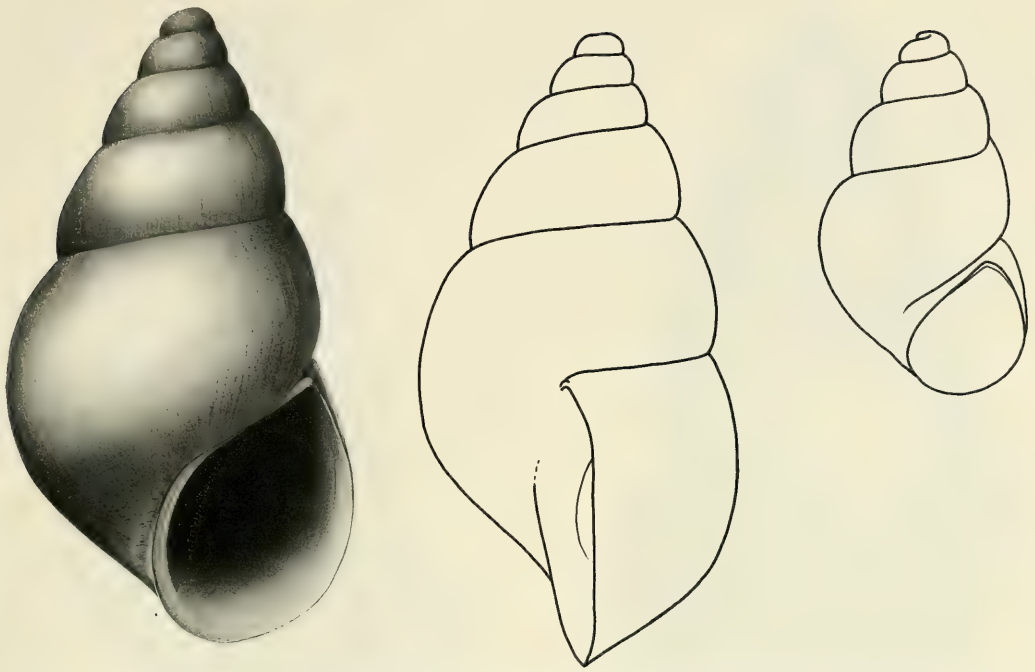


Fig. 3. *Heleobops clytus,* new species. The holotype, UF 175170 (4.1 mm), is shown on the left (both views) while a small paratype male, UF 135428, is shown to the right (same scale as above).

suture, although this distinction is hardly sufficient to warrant specific recognition. It differs anatomically by various features of the male penis. The penis is stout and cylindrical with three–five apocrine glands along the outer curvature, and with a small terminal papilla. The distal-most gland usually is separated from the others and is raised slightly higher. The penis lacks a basal expansion along the outer curvature, and lacks a lobe along the inner curvature near the terminus. In *H. docimus* the penis is long and tapered distally, and has a conspicuous swelling at the base along the outer curva-

Table 3.—Shell parameters for *Heleobops clytus.* $\bar{X}$ = mean, *SD* = standard deviation.

	SH	SW	ApH	ApW	Wh	$\frac{SW}{SH}$	$\frac{ApH}{SH}$	$\frac{ApW}{ApH}$
Holotype	4.1	2.2	1.7	1.3	5.5	0.54	0.42	0.76
Paratypes, ♀, n = 16								
$\bar{X}$	3.8	2.0	1.6	1.2	5.8	0.52	0.42	0.73
SD	0.3	0.1	0.1	0.1	0.2	0.0	0.0	0.0
Minimum	3.2	1.7	1.5	1.1	5.1	0.47	0.40	0.69
Maximum	4.2	2.2	1.7	1.3	6.0	0.56	0.46	0.83
Paratypes, ♂, n = 12								
$\bar{X}$	2.8	1.5	1.2	1.0	4.0	0.55	0.45	0.77
SD	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0
Minimum	2.7	1.5	1.2	0.9	3.7	0.52	0.44	0.75
Maximum	2.9	1.6	1.3	1.0	4.2	0.58	0.46	0.79

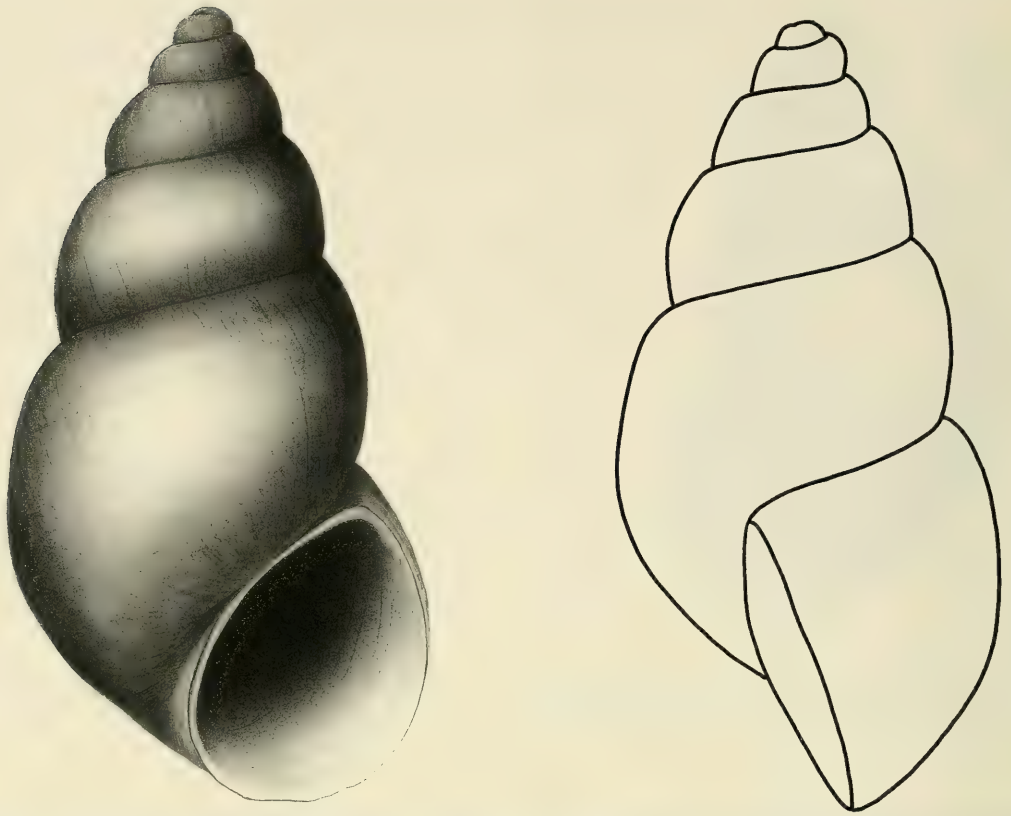


Fig. 4. *Pyrgophorus coronatus bermudezi* (Aguayo), UF 175165, spring 2 km east-southeast of Duverge, Independencia Province, Dominican Republic. Shell height, 3.7 mm.

ture. It bears a large lobe along the inner curvature near the terminus, which causes the penis to appear bifurcate. It has two–five apocrine glands along the right margin near the base and a terminal papilla.

Heleobops clytus was found with *Pyrgophorus coronatus bermudezi* (Aguayo, 1947). The latter was described from Pleistocene specimens from Lago de Enriquillo and is common both in the lake and in springs draining to the lake. The holotype is an obese individual with spines on the periphery of the shell, as occurs in some individuals of most forms of *Pyrgophorus.* Most specimens of *bermudezi* lack spines and are more slender. Such specimens are very similar in shell features to *H. clytus,* except that the whorls are more rotund with a deeper suture, the peristome is complete in adults, and the umbilicus is narrowly rimate (Fig. 4).

Etymology.—The genus name *Heleobops,* originally treated as feminine (Thompson 1968:22), herein is amended to masculine gender in accordance with ICZN Article 30 (ii). The species name *clytus* is from the Classical Greek *klytos,* meaning renowned, and refers to the fact that the species is from the first land in the New World discovered by eastern explorers.

Heleobops torquatus, new species
Fig. 5, Table 4

Description.—Shell sexually dimorphic. Females elongate-conic with attenuated apex; spire nearly straight-sided. Mature shells 2.7–3.2 mm tall; width/height, 47–

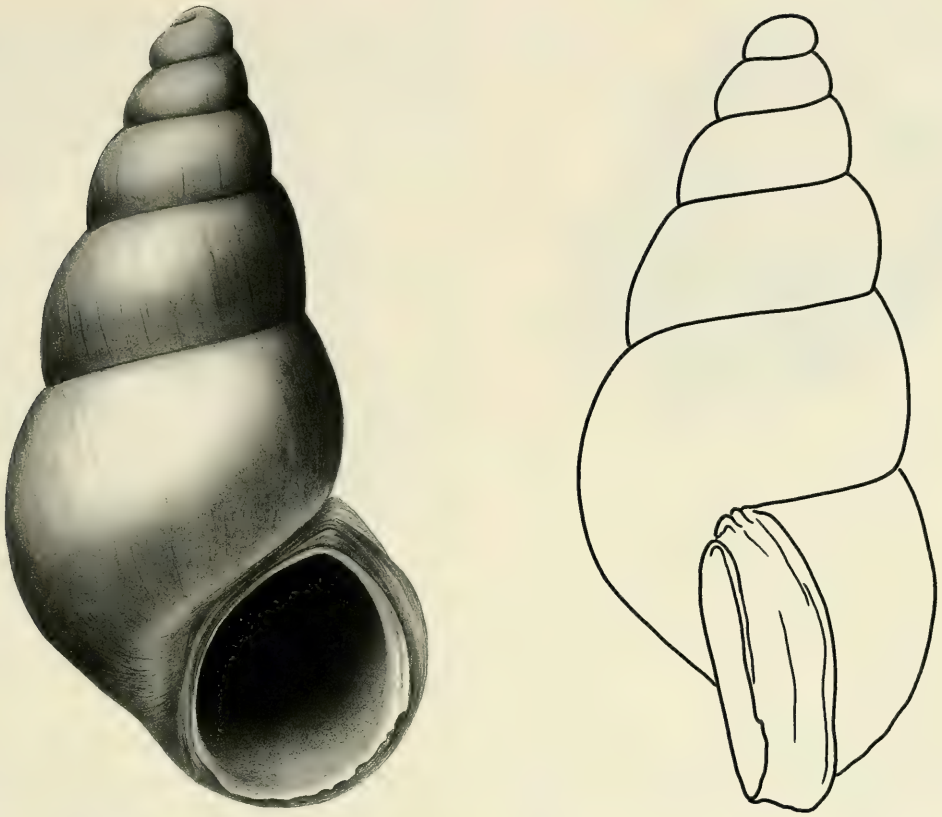


Fig. 5. *Heleobops torquatus,* new species, holotype, UF 175256. Shell height, 2.9 mm.

53%. Adults having 5.4–6.0 whorls. Body whorl with a heavy varix forming a collar behind aperture. Apical whorl strongly protruding; 0.23–0.25 mm in diameter. Suture on subsequent whorls strongly impressed. Periostracum light gray. Shell transparent; smooth, with very faint microsculpture of collabral striations and weaker spiral stri-

Table 4.—Shell parameters for *Heleobops torquatus.* $\bar{X}$ = mean, *SD* = standard deviation.

	SH	SW	ApH	ApW	Wh	$\frac{SW}{SH}$	$\frac{ApH}{SH}$	$\frac{ApW}{ApH}$
Holotype	2.9	1.3	1.0	0.84	6.0	0.45	0.34	0.84
Paratypes, ♀, *n* = 10								
$\bar{X}$	2.8	1.5	0.93	0.81	5.6	0.52	0.33	0.86
SD	0.0	0.1	0.0	0.0	0.2	0.0	0.0	0.0
Minimum	2.4	1.3	0.84	0.71	5.4	0.47	0.30	0.81
Maximum	3.2	1.6	0.99	0.87	6.0	0.53	0.34	0.90
Paratypes, ♂, *n* = 10								
$\bar{X}$	2.3	1.2	0.81	0.65	5.0	0.55	0.36	0.81
SD	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.1
Minimum	2.1	1.1	0.74	0.59	4.8	0.50	0.32	0.70
Maximum	2.4	1.4	0.84	0.68	5.2	0.57	0.40	0.85

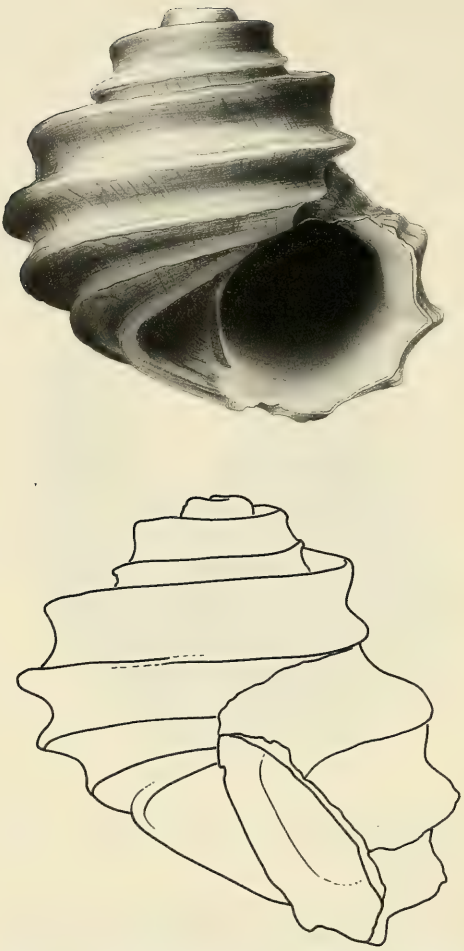


Fig. 6. *Lithococcus aletes,* new species, holotype, UF 36378. Shell height, 2.4 mm.

ations. Immature shells imperforate; mature shells rimate behind columellar lip. Aperture ovate; width/height, 81–90%; height 30–34% of shell height; posterior corner weakly angled. Peristome thick; complete across parietal margin where it forms a heavy parietal callus. Males similar to females but smaller and tending to be ventricose; 2.1–2.4 mm long and with 4.8–5.2 whorls.

The measured (below) height and width of shell include the expansion of the collar-like callus behind the peristome. The height and width of the aperture were determined from the outer edges of the peristome.

The penis is a simple, elongate, blade-like structure lacking an expansion at the base of the outer curvature and a non-glandular lobe on the inner curvature near the terminus. It also lacks a terminal papilla. The outer curvature bears only two apocrine glands.

Type locality.—A marshy stream 2.6 km northeast of Snipe, St. Elizabeth Parish, Jamaica. Holotype: UF 175256; collected 31 Aug 1976 by Fred G. Thompson. Paratypes: UF 135427, USNM 860567, numerous specimens; same data as the holotype. The stream was clear and about one meter deep with a fine silt bottom over clay and limestone. *Heleobops torquatus* was collected by sifting aquatic vegetation.

Remarks.—This species is readily distinguished from other known *Heleobops,* as well as all other West Indian Hydrobiidae, by the collar-like varix behind the aperture. The male penis also is unique within the genus.

Etymology.—The species name is derived from the Latin, *torquatus,* meaning adorned with a collar or necklace.

Lithococcus aletes, new species
Fig. 6

Description.—Shell very small for genus, broadly ovate, slightly wider than high. Periostracum light brown. Narrowly umbilicate. Whorls, 4.0. Apical whorl planular. Protoconch consisting of a single whorl; rounded; sculptured with fine collabral striations. Teleoconch bearing six heavy spiral crests. Superimposed on and between these are numerous fine spiral threads and coarser, uneven transverse threads. Uppermost crest forming a dished shoulder on the whorls. Second crest largest and forming periphery of shell. Lower four crests diminishing in size toward the base. Aperture slightly wider than high; prosocline at an angle of 30° to coiling axis. Peristome complete across parietal wall and broadly adnate to previous whorl; outer and basal margins

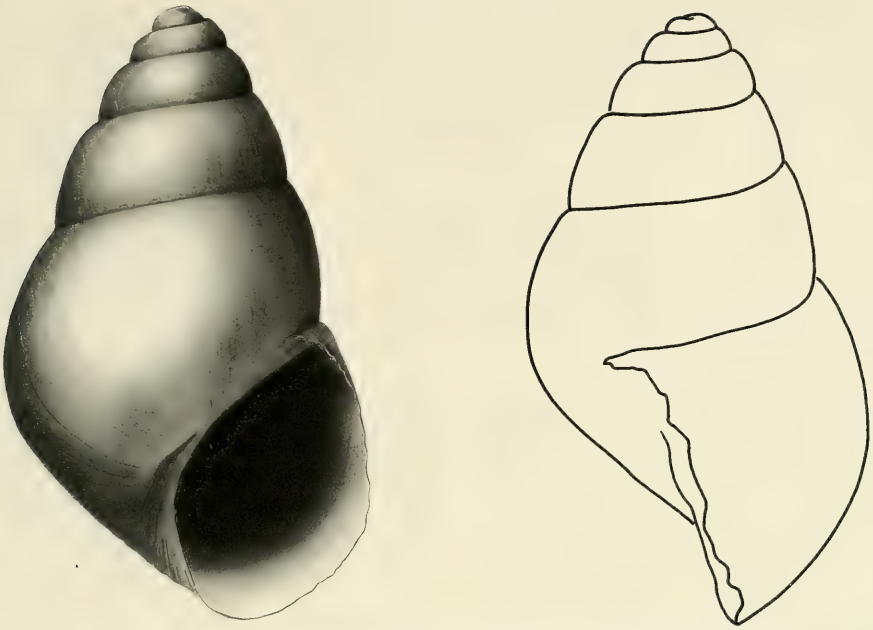


Fig. 7. *Littoridina microcona,* new species, holotype, UF 175912. Shell height, 2.9 mm.

very thick. Shell height, 2.4 mm; shell width, 2.5 mm; aperture height, 1.1 mm; aperture width 1.2 mm.

Type locality.—Rio Baru, 0.5 km above mouth of river, Dominical, Puntarenas Province, Costa Rica. Holotype: UF 36378; collected 12 Jul 1963 by Fred G. Thompson.

Remarks.—This species differs from other *Lithococcus* by its much smaller size, and the smooth crests on the surface of the shell whorls. *Lithococcus multicarinatus* (Miller, 1879) and *L. venustus* Pilsbry, 1950 are about 10 mm in diameter as adults, and have spiral series of knobs on the crests forming a multiple corona on the shell.

This species is known only from the holotype. It is described because it adds greatly to the known geographic distribution of the genus, and because of the distinctiveness of its shell. The microsculpture of the shell leaves little doubt about its generic assignment. The holotype was found in debris on the bottom of a quiet pool at the side of the Rio Baru, along with numerous live *Cochliopa* and *Zetekina.* The Rio Baru is a high-gradient river whose headwaters originate at about 3000 m elevation. The river lies below 100 m only along the lower 4–5 km of its course, where it consists of series of rocky rapids separated by quieter sand- and gravel-bottomed pools. The shell probably was washed downstream from a population living at higher elevation. Such an occurrence would be consistent with the known ecology of other *Lithococcus,* which occur in low-gradient freshwater zones of rivers above the influence of tidal fluctuations.

Etymology.—From *aletes,* Greek, a vagrant, and referring to the origin of the holotype.

Littoridina microcona, new species
Fig. 7, Table 5

Description.—Small, about 2.4–2.9 mm long; conical; width/height, 49–58%. Apex depressed, rounded; first whorl (apex) weakly protruding; spire convex in outline along earlier whorls; last two whorls nearly flat-

Table 5.—Shell parameters for *Littoridina microcona*. $\bar{X}$ = mean, *SD* = standard deviation.

	SH	SW	ApH	ApW	Wh	$\frac{SW}{SH}$	$\frac{ApH}{SH}$	$\frac{ApW}{ApH}$
Holotype	2.9	1.7	1.3	1.0	6.0	0.58	0.44	0.76
Paratypes, $n = 10$								
$\bar{X}$	2.6	1.5	1.1	0.9	4.8	0.57	0.44	0.75
SD	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Minimum	2.4	1.4	1.1	0.8	4.5	0.49	0.42	0.71
Maximum	2.9	1.6	1.3	0.9	5.0	0.53	0.46	0.81

sided; last whorl with a weak peripheral keel. Whorls, 4.5–5.0; apical whorl 0.15–0.16 mm in diameter. Periostracum grayish-yellow. Sculpture of very fine collabral striations and finer, sparce spiral microstriations. Umbilicus rimate; partially obstructed by reflected columellar lip. Aperture ovate; width/height, 71–81%; height 42–46% of shell height. Plane of aperture inclined 27–28° to coiling axis. Peristome thin, sharp, incomplete across parietal margin.

Type locality.—Marshy pool 1.0 km north of Boca de Barranca, Puntarenas Province, Costa Rica. Holotype: UF 175912; collected 19 Jun 1963 by Fred G. Thompson. Paratypes: UF 37799, USNM 860568, numerous specimens; same data as the holotype. The pool was about 10–30 cm deep with a mud-gravel bottom. The water was slightly brackish and turbid with visibility restricted to only a few centimeters. Snails were found crawling on dead grasses in shallow water.

Remarks.—*Littoridina* includes four known species: *L. quadichaudi* Souleyet, 1852; *L. crosseana* (Pilsbry, 1910); *L. orcutti* (Pilsbry, 1928); and the novelty described herein. Most other hydrobiids referred to *Littoridina* now are placed in *Heleobia* (Hershler & Thompson 1991). *Littoridina microcona* is similar in shell shape to *L. quadichaudi* from Ecuador. It differs from all *Littoridina* by its very small size and rather blunt apex. The penis most resembles that of *L. orcutti* from southwestern Mexico by having a single papilla along the inner curvature that bears numerous smaller glandular papilla. It differs from *L. orcutti* also by having several small, slender papillae along the outer curvature near the base.

Etymology.—The species name *microcona* refers to the small cone-shaped shell of this snail.

Mesobia, new genus

Type species.—*Mesobia pristina*, new species.

Description.—Shell slender; sexuall dimorphic in shape and size. Adult females elongate-conic, about 2.8–3.0 mm long and with about five whorls. Adult males about half as long as females, more broadly conical in shape and with about 3.5 whorls. Apical whorl protruding, about 0.25 mm in diameter. Teleoconch suture deeply impressed. Protoconch slightly wrinkled. Teleoconch sculpture of collabral striations. Peristome complete in adult specimens, simple. Aperture nearly round. Umbilical perforation open. Operculum broadly ovate, paucispiral. Central radular teeth with 2 pairs of basal cusps inserting into lateral angles; lateral angles moderately expanded, ventral process well excavated. Animal pale, epithelial pigment typically restricted to digestive gland. Dorsal surfaces of cephalic tentacles with longitudinal ciliary tracts; left tentacles having transverse ciliary bands. Ctenidial filaments about 35. Osphradium about 33% of ctenidial length. Stomach without posterior caecal chamber. Females

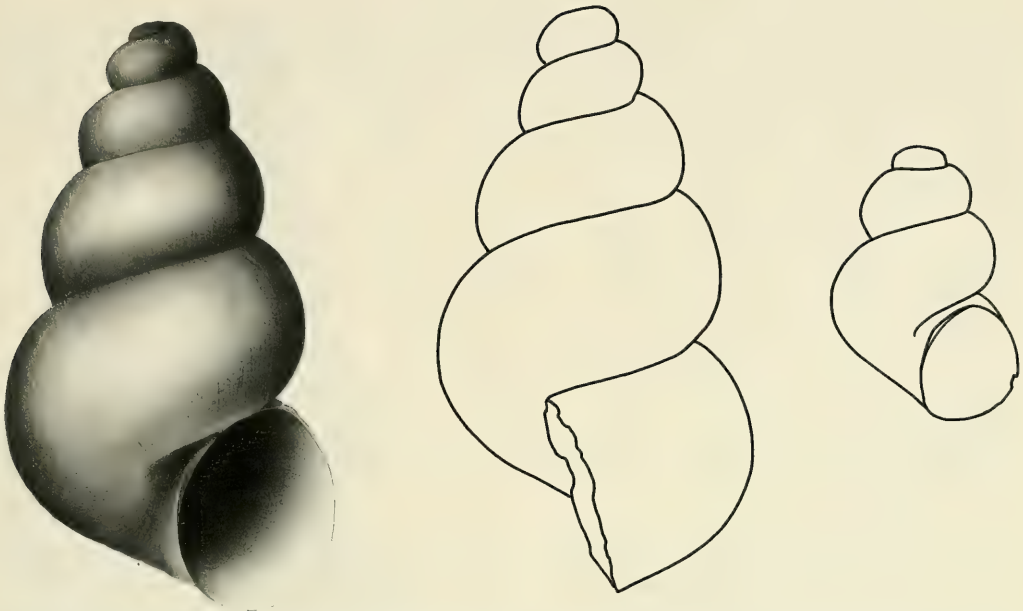


Fig. 8. *Mesobia pristina,* new genus and new species. The holotype, UF 175031 (2.8 mm), is shown on the left (both views) while a small paratype male, UF 40421, is shown to the right (same scale as above).

ovoviviparous. Small, simply lobate ovary lying against posterior edge of stomach. Capsule gland an enlarged, thin-walled, brood pouch having slightly muscularized opening. Albumen gland small, folded lateral to capsule gland. Sperm sacs small, pouch-like, broadly overlapping, pressed against left side of albumen gland. Ducts of sperm sacs long, narrow. Duct of seminal receptacle connecting to oviduct just distal to point where latter opens into albumen gland; distal to this a short fertilization duct connects with distal end of duct of bursa copulatrix. Sperm tube short, non-muscular. Embryos numerous, small-sized. Small, simply lobate testis lying against posterior edge of stomach. Prostate gland small, almost entirely non-pallial; vas deferens exiting just proximal to anterior tip of gland. Penis moderate-sized, narrow, with slender non-glandular lobe issuing from inner curvature near distal tip; tip blunt, with terminal papilla. Penis bearing single, small, apocrine glands on outer and inner curvature basally.

Remarks.—Although the shell of *Mesobia* resembles that of *Durangonella,* characteristics of genitalia preclude a close relationship. The presence of apocrine glands on the penis places *Mesobia* in the group of *Heleobia* and related genera. While the penis of *Mesobia* closely resembles those of some *Heleobops,* the former is distinguished from all other genera in this group by its ovoviviparous reproductive mode, and by females having a prominently twisted albumen gland and very small sperm pouches.

Mesobia pristina, new species
Fig. 8, Table 6

Description.—Shells sexually dimorphic. Females slender; elongate-conic; about 2.8–3.2 mm long; width/height, 49–59%. Spire nearly straight-sided or weakly convex in outline. Thin and transparent. Periostracum light grayish-brown. Teleoconch sculpture of very fine collabral striations. Apical whorl protruding, 0.24–0.26 mm in diam-

Table 6.—Shell parameters for *Mesobia pristina*. $\bar{X}$ = mean, *SD* = standard deviation.

	SH	SW	ApH	ApW	Wh	$\frac{SW}{SH}$	$\frac{ApH}{SH}$	$\frac{ApW}{ApH}$
Holotype	2.8	1.5	0.91	0.75	5.0	0.55	0.32	0.83
Paratypes, ♀, *n* = 13								
$\bar{X}$	2.9	1.5	0.92	0.78	5.0	0.53	0.32	0.85
SD	0.1	0.1	0.0	0.0	0.2	0.0	0.0	0.0
Minimum	2.8	1.4	0.87	0.74	4.8	0.49	0.30	0.80
Maximum	3.2	1.6	0.96	0.81	5.3	0.59	0.34	0.93
♂, *n* = 10								
$\bar{X}$	1.5	1.0	0.64	0.56	3.5	0.66	0.43	0.85
SD	0.1	0.1	0.0	0.0	0.2	0.0	0.0	0.0
Minimum	1.4	0.9	0.59	0.50	3.2	0.60	0.40	0.81
Maximum	1.6	1.1	0.68	0.59	3.9	0.69	0.46	0.90

eter. Whorls 4.8–5.3 in adults; suture deeply impressed. Umbilicus broadly perforate; opening partially obstructed by columellar margin of peristome. Aperture height 30–34% of shell height; broadly ovate, width/height, 80–93%; posterior corner broadly rounded, not angular. Apertural plane inclined 21–22° to coiling axis. Peristome complete across parietal margin of aperture and narrowly in contact with or occasionally free from previous whorl. Lip thin and sharp; simple, not reflected nor with internal callus; outer basal margin slightly advanced. Males smaller than females, about 1.4–1.6 mm long; more broadly conic, width/height, 60–69%. Whorls fewer, 3.2–3.9 in adults; last whorl tending to become ventricose. Aperture relatively larger and more nearly rounded; height 40–46% of shell height; height/width, 81–90%; nearly always solute from previous whorl in adults.

Type locality.—Lago de Yajoa, at the north side of an island near Agua Azul, Cortez Province, Honduras. Holotype: UF 175031; collected 29 Aug 1964 by Fred G. Thompson. Paratypes: UF 40421, USNM 860569, numerous specimens; same data as the holotype. The type locality is a small cove on the north side of a small island near Agua Azul. The water was about 3 m deep and was clear to the bottom. Snails were collected by washing filamentous algae. The algae formed large floating mats amid aquatic angiosperms of the genera *Nuphar, Eichornia, Myriophyllum, Utricularia* and *Scirpus.*

Etymology.—The name *Mesobia* (feminine) is taken from Meso America and the Classical Greek *bios,* and refers to the geographic occurrence of the genus. The species name *pristina* is from the Latin *pristinus,* meaning primitive, and refers to the relationship of *Mesobia* to *Heleobia* and allies.

Texapyrgus, new genus

Type species.—*Texapyrgus longleyi,* new species.

Description.—Shell minute, elongate-conic to turreted. Apical whorl protruding, about 0.16 mm in diameter perpendicular to initial suture. Teleoconch sutures deeply impressed. Protoconch surface coarsely wrinkled. Teleoconch sculpture of numerous, strong, evenly spaced spiral lines; collabral striations weaker. Peristome complete in adult specimens, simple. Aperture ovate. Umbilical perforation open. Operculum broadly ovate, paucispiral. Central radular teeth with single pair of large basal cusps inserting into region where lateral angles originate. Lateral angles moderately ex-

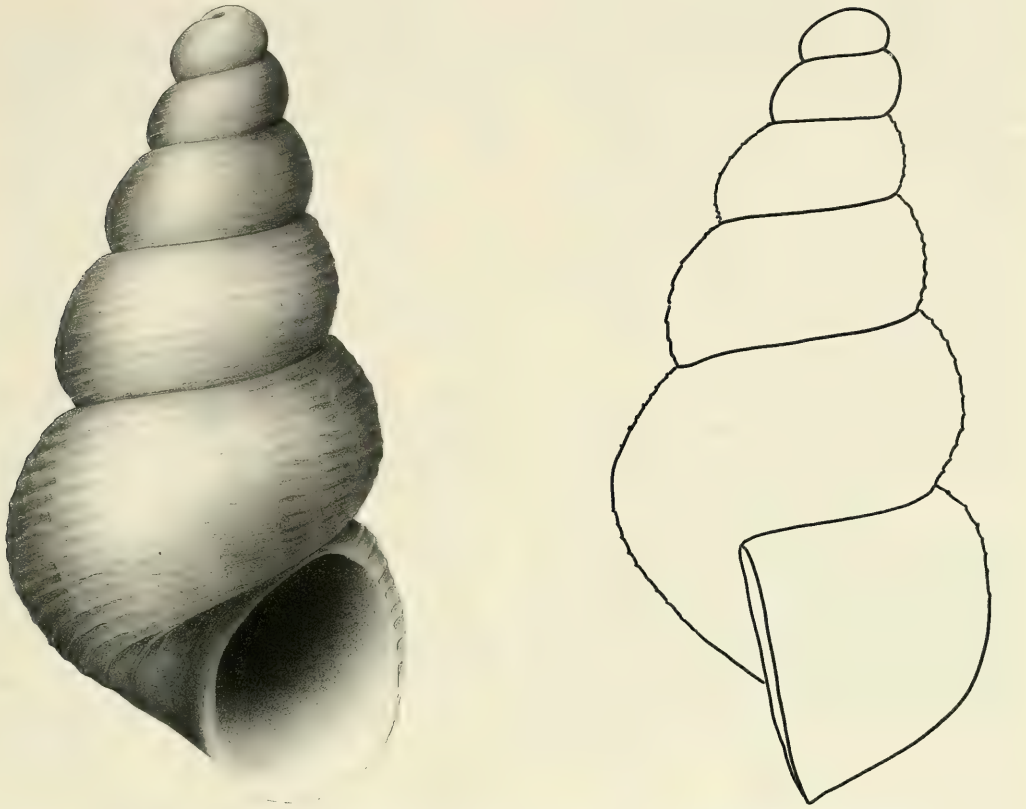


Fig. 9. *Texapyrgus longleyi,* new genus and new species, holotype, USNM 860551. Shell height, 1.6 mm.

panded; ventral process well excavated. Animal blind, unpigmented. Cephalic tentacles without ciliary bands or tracts. Ctenidial filaments about 10. Osphradium about a third as long as ctenidium, extending to near posterior end of ctenidium. Females oviparous. Ovary a large simple sac. Albumen gland with short posterior bend. Bursa copulatrix absent. Small seminal receptacle pressed against right side of coiled oviduct. Oviduct connecting with anterior edge of folded albumen gland via a short duct and coursing anteriorly as non-muscular sperm tube. Short duct from seminal receptacle opening into oviduct slightly anterior to above. Sperm tube joining anterior capsule gland; genital aperture slightly muscularized. Testis of numerous, simple lobes posterior to stomach. Prostate gland small, with very shortpallial portion; vas deferens exiting from base of blunt anterior edge of gland. Penis elongate, tapering, with single stalked apocrine gland on outer curvature near midlength.

Remarks.—The presence of an apocrine gland on the penis places *Texapyrgus* in the group of *Heleobia* and related genera. *Texapyrgus* most closely resembles *Balconorbis* anatomically, but differs in various shell features and by females having a sperm pouch.

Texapyrgus longleyi, new species
Fig. 9, Table 7

Description.—Shell height, 1.4–1.8 mm. Male shells slightly smaller and narrower than those of females. Spire nearly straight,

Table 7.—Shell parameters for *Texapyrgus longleyi*. $\bar{X}$ = mean, *SD* = standard deviation.

	SH	SW	ApH	ApW	Wh	$\frac{SW}{SH}$	$\frac{ApH}{SH}$	$\frac{ApW}{ApH}$
Holotype	1.6	0.82	0.50	0.40	5.5	0.51	0.31	0.80
Paratypes, $n = 9$								
$\bar{X}$	1.5	0.77	0.47	0.39	5.2	0.53	0.32	0.84
SD	0.1	0.1	0.0	0.0	0.2	0.0	0.1	0.0
Minimum	1.4	0.69	0.42	0.36	5.0	0.51	0.30	0.77
Maximum	1.6	0.85	0.53	0.46	5.5	0.55	0.34	0.90

although sometimes slightly concave or convex depending on position of body whorl. Thin and transparent. Periostracum light brown. Protoconch, 1.0–1.25 whorls, protruding, slightly tilted, with strongly wrinkled surface that becomes smooth on early teleoconch; protoconch diameter, about 0.16 mm. Spiral lines prominent on teleoconch, crossed occasionally by strong collabral striae. Twenty–thirty spiral lines on body whorl, extending from suture into umbilical area. Whorls, 5.0–5.5 in adults; sutures deeply impressed. Umbilicus perforate; opening sometimes constricted by columellar margin of aperture. Aperture 30–34% of shell height, broadly ovate, width/height, 77–90%; broadly rounded below, slightly angled above. Apertural plane near parallel to coiling axis. Peristome complete across parietal margin and narrowly in contact with previous whorl. Lip thin, sharp, very slightly reflected along inner margin.

Type locality.—Spring on east side of Devils River in canyon just downflow from Slaughter Bend, Amistad National Recreation Area, about 32 km north of Del Rio, Val Verde County, Texas, United States (Hershler & Longley 1987, fig. 2). Holotype: USNM 860551; collected by R. Hershler and Susannah Corona, Aug 1986 (from series of pooled samples). Paratypes: UF 172632, USNM 860552, numerous specimens; same data as the holotype. The type locality is a small rheocrene discharging directly into the Devils River. The spring had a gravel bottom and lacked aquatic vegetation. Snails and other phreatic animals were collected by placing a fine mesh net into the main spring orifice and then periodically removing and washing the net. Other phreatic fauna included *Phreatodrobia coronae* Hershler & Longley, 1987 and various crustaceans.

Etymology.—The name *Texapyrgus* (masculine) is taken from Texas and the Classical Greek *pyrgos*, meaning tower, and refers to the geographical occurrence of the genus and its elongate shell. The species is named after Glenn Longley of the Edwards Aquifer Research and Data Center (Southwest Texas State University), who provided logistical support for the second author's fieldwork in Texas.

Acknowledgments

Fieldwork was supported, in part, by a Smithsonian Institution Scholarly Studies Award to the authors. The National Park Service supported Hershler's fieldwork in the Amistad National Recreation Area. Shells were drawn by Ms. M. Ryan, Department of Invertebrate Zoology, National Museum of Natural History.

Literature Cited

Aguayo, C. G. 1947. Notes y Variedades (VIII).—Revista de la Sociedad Malacologica "Carlos de la Torre" 5:81–83.

Golikov, A. N., & Y. I. Starobogatov. 1975. Systematics of prosobranch gastropods.—Malacologia 15:185–232.

Hershler, R., & G. Longley. 1987. *Phreatodrobia co-*

ronae, a new species of cavesnail from southwestern Texas.—Nautilus 101:133–139.

———, & F. G. Thompson. 1991. A review of the genera of the aquatic gastropod subfamily Cochliopinae (Prosobranchia: Hydrobiidae).—Malacological Review (in press).

Ioganzen, B. G., & Y. I. Starobogatov. 1982. A finding of a freshwater mollusc of the family Triculidae (Gastropoda, Prosobranchia) in Siberia.—Zoologicchesky Zhurnal 61:1141–1147.

Miller, K. 1879. Die Binnenmollusken von Ecuador.—Malakozoologische Blatter 1:117–203.

Parodiz, J. J. 1969. The Tertiary non-marine Mollusca of South America.—Annals of the Carnegie Museum 40: 1–242.

Pilsbry, H. A. 1910. New Amnicolidae of the Panuco River system, Mexico.—Nautilus 23:97–100.

———. 1928. Mexican mollusks.—Proceedings of the Academy of Natural Sciences of Philadelphia 80:115–117.

———. 1950. Fresh water mollusks from Colombia and Guatemala.—Nautilus 63:82–85.

Ponder, W. F., & A. Warén. 1988. Appendix. Classification of the Caenogastropoda and Heterostropha—a list of the family-group names and higher taxa.—Malacological Review, Supplement 4:288–326.

Souleyet, M. 1852. Mollusques. *In* Voyage autour du monde execute Penant les annes 1836 et 1837 sur la corvette la bonite commandée par M. Vaillant Capitaine de Vaisseau Publié par ordre du gouvernement sous les auspices du département de la marin. Zoologie par M.M. Eydoux et Souleyet. Volume 2, Arthus Bertrand, Paris, 664 pp.

Thiele, J. 1928. Revision des systems Hydrobiiden und Melaniiden.—Zoologische Jahrbucher 55: 351–402.

Thompson, F. G. 1968. The aquatic snails of the family Hydrobiidae of peninsular Florida.—University of Florida Press, Gainesville, 268 pp.

Troschel, F. H. 1856–1863. Das Gebiss der Schnecken zur Bergründung einer Natürlichen Classification. Volume 1.—Nicolaische Verlagsbuchhandlung, Berlin, 252 pp.

Tryon, G. W. 1866. [Review of] Researches upon the Hydrobiinae and allied forms.—American Journal of Conchology 2:152–158.

(FGT) Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, U.S.A.; (RH) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 684–687

REDESCRIPTION OF *HELMETOPHORUS RANKINI* HARTMAN, 1978 (POLYCHAETA: HELMETOPHORIDAE) AND ITS TRANSFER TO THE FLABELLIGERIDAE

Christopher J. Glasby and Kristian Fauchald

Abstract.—The only representative of the Helmetophoridae, *Helmetophorus rankini* Hartman, 1978, is redescribed and transferred to the Flabelligeridae. The species shares in common with the Flabelligeridae a papillated body surface, a buccal region with branchiae and grooved palps that is covered (partially) by a cephalic hood, weakly developed parapodia, and cross-barred capillaries.

The Helmetophoridae is currently represented by a single species, *Helmetophorus rankini* Hartman, 1978, collected from the Weddell Sea, Antarctica in 3111 m. The species has not been recorded since the original description. During a recent study of phylogenetic relationships of nereidoid polychaetes by CJG, it was found that Helmetophoridae was assigned to the order Phyllodocida: superfamily Nereidoidea by George & Hartmann-Schröder (1985:23). The classification of the Helmetophoridae was influenced by Hartman's (1978) opinion that *H. rankini* resembled the Hesionidae in having the first three segments with tentacular cirri, a muscular eversible proboscis, and biramous parapodia. We have examined the type specimens of *H. rankini,* plus an additional specimen from near the type locality, and find that this species should be transferred to the order Flabelligerida: family Flabelligeridae.

Order Flabelligerida
Family Flabelligeridae
Saint-Joseph, 1894
Genus *Helmetophorus* Hartman, 1978

Type species.—*Helmetophorus rankini* Hartman, 1978 by monotypy.

Diagnosis.—Flabelligerids with buccal apparatus (prostomium and peristomium) partially covered by cephalic hood. Oral tube non-retractile, cylindrical and muscular. Branchiae, 5 pairs, of 2 types: 3 pairs clavate-cirriform, arising from reduced branchial membrane; 2 pairs foliaceous, arising posteroventrally to branchial membrane. First parapodia lacking neuropodia (and neurosetae), subsequent ones with both neuropodia and notopodia. All setae cross-barred capillaries. Anterior setae directed forward, but not prolonged and cage-forming.

Remarks.—The most remarkable feature of this genus is the prominent oral tube, which appears not to be retractable. Other flabelligerids having an oral tube include *Buskiella* McIntosh, 1885; *Therochaeta* Chamberlin, 1919; and *Therochaetella* Hartman, 1967. *Helmetophorus* differs in lacking a true cephalic cage, and in having an extremely reduced branchial membrane with few branchial filaments. The genus also shows some resemblance to *Diplocirrus* Haase, 1915, in having branchial filaments of two types; however, *Diplocirrus* has 4 pairs of branchiae (Fauchald 1977:116). The generic groupings within the Flabelligeridae are poorly understood (Chamberlin 1919: 397, Fauchald 1972:213), and it is not possible to further evaluate the relationship of *Helmetophorus* within the family at this time.

Helmetophorus rankini Hartman
Fig. 1a–d

Helmetophorus rankini Hartman, 1978:145, fig. 11a–f.

Material examined.—Holotype: USNM 46748, Antarctic Ocean, Weddell Sea, 73°28.4′S, 30°26.9′W, USCGC *Glacier* Cr. 2, Sta. 22, 3111 m, coll. J. S. Rankin, 13 Mar 1969. Paratypes: 4 (USNM 46749), collection details as for holotype. Non-type: 1 (USNM 97424), Antarctic Ocean, Weddell Sea, 73°52′S, 31°18′W, USCGC *Glacier* Cr. 2, Sta. 21, 2288 m, coll. J. S. Rankin, 13 Mar 1969, det. K. Fauchald.

Description.—Holotype complete with 22 setigers, 6.5 mm long, 0.8 mm wide maximally; left 4th parapodium removed, not 3rd as indicated by Hartman (1978: fig. 11d); moderately-well preserved, many setae damaged.

Body inflated anteriorly, widest at setiger 9, tapering greatly after setiger 12 to well defined tail; color in alcohol white, setae clear; body papillae minute (18–24 μm long), clavate, sparsely covering dorsum and ventrum, more abundant on parapodia with additional 2–3 larger papillae (0.1–0.4 mm long) on presetal and/or postsetal lips (Fig. 1c, d); mucous coat or encrusted sand grains absent.

Prostomium rounded dorsally, ill-defined anteriorly merging into oral tube; eye-spots absent (Fig. 1a). Oral tube cylindrical, muscular with pair of inner dorsal lips arranged in sagittal plane, separated by deep medial groove (Fig. 1b). Palpal scars anterolateral to prostomium (Fig. 1a, b). Cephalic hood helmet-like dorsally, low and collar-like ventrally, extending anteriorly to branchial membrane (Fig. 1a). Branchial membrane ridge-like, convoluted laterally, extending across dorsum behind prostomium posteriorly (Fig. 1a, b). Branchiae, 5 pairs, arranged as follows (B4 and B5 absent in holotype, arrangement inferred by scars): B1 arising laterally from anterior end of branchial membrane; B2 arising dorsolaterally from dorsal crest in branchial membrane; B3 arising posterior to B2 from branchial membrane between ventral loop and mid-dorsal region; B4 arising laterally just below ventral loop of branchial membrane; and B5 arising just dorsolaterally to B4 (Fig. 1a, b).

Parapodia low, first pair with notopodia only, remaining pairs with both noto- and neuropodia; anterior parapodia directed anterolaterally (Fig. 1a), posterior parapodia directed posterolaterally. Notopodia and neuropodia with small retractile conical lobes and small bundles of setae; distance between noto- and neuropodia similar throughout (Fig. 1c, d). True aciculae absent, although 6 or so fine, short internal spines present ventral to neurosetae (Fig. 1c, d).

All setae cross-barred capillaries, posterior ones appearing to have tips with weaker bars (Fig. 1c, d); setae of parapodia in mid-body generally slightly longer than those of anterior and posterior parapodia. Notosetae and neurosetae similar within parapodium, with 3–7 capillaries in each bundle, varying in basal width (3.5–8.8 μm) and length (about 0.5 to almost 2 times body width).

Anus terminal; no indication of anal cirri.

Variation.—Paratypes approximately same size and numbers of setigers as holotype, generally poorly preserved. Body widest over setigers 6–9. Head region more extended (i.e., cephalic hood retracted) than in holotype, exposing smooth posterior buccal region. B1–B3 usually absent or damaged; B4, B5 absent, branchial scars difficult to discern. Non-type specimen with B4 present, foliaceous, similar in length to clavate-cirriform type; one palp present, weakly grooved, extending just beyond oral tube.

Remarks.—Since Hartman (1978) considered this species to resemble Hesionidae, her terminology and interpretation of certain head-end characters reflected that opinion. For example, she considered the first four segments to be achaetous, with segments 1–3 each having a pair of tentacular

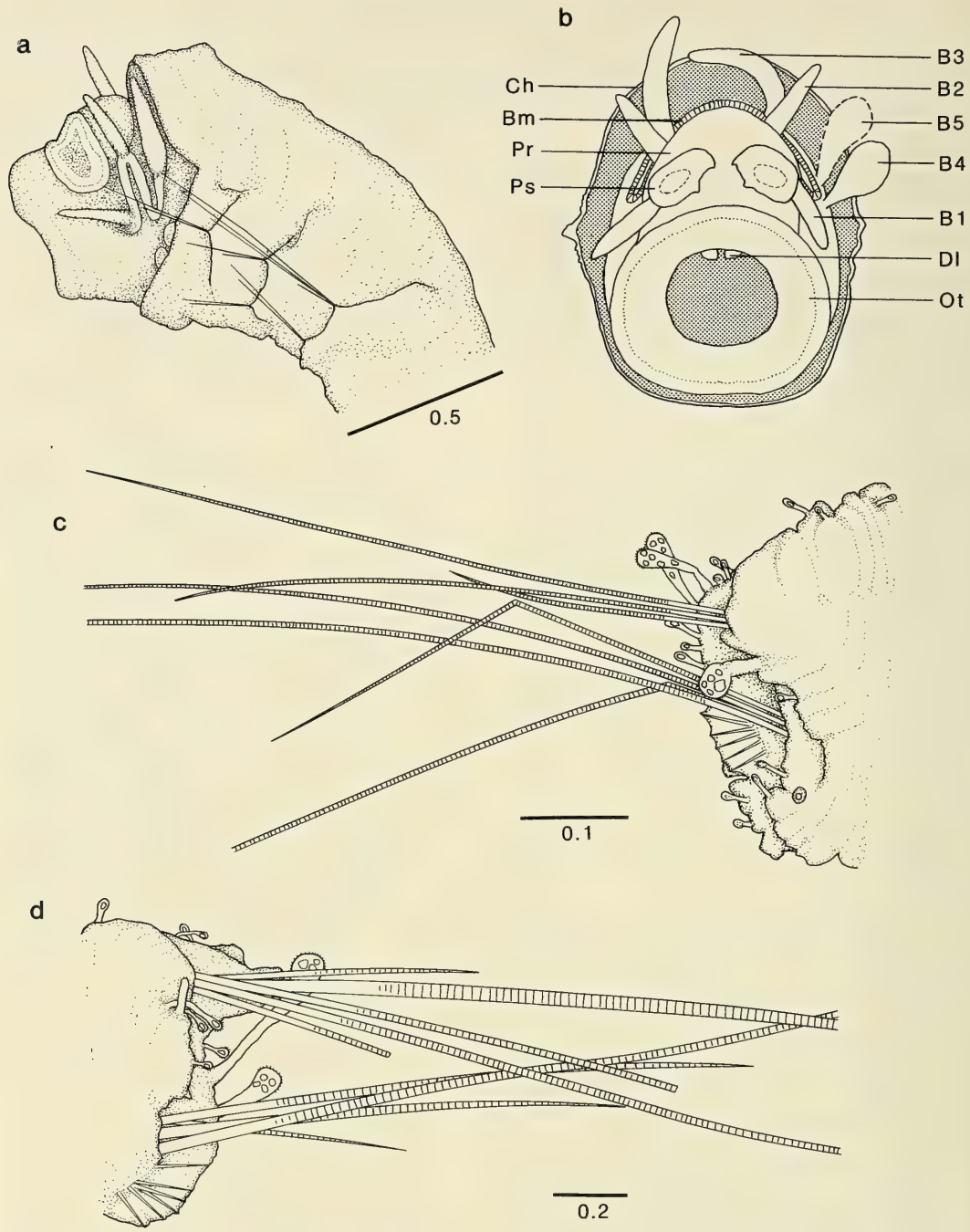


Fig. 1. *Helmetophorus rankini:* a, Holotype, head-end, lateral view (B1, B2 illustrated from other material; B4, B5 absent, scars only visible); b, Diagrammatic representation of head-end, frontal view (B4, B5 of left-side not shown); c, Paratype, left parapodium 6, posterior view; d, Paratype, left parapodium 15, anterior view. Abbreviations: B1–B5 = branchiae; Bm = branchial membrane; Ch = cephalic hood; Dl = dorsal lip; Ot = oral tube; Pr = prostomium; Ps = palpal scar. All scale bars in mm.

cirri and segment 4 being long and necklike. These so-called segments are here considered to be a part of the buccal apparatus (i.e., pre-segmental), and her tentacular cirri are interpreted as branchiae. Hartman overlooked the branchial scars of the posterior 2 pairs of branchiae (B4, B5).

There remain some questions concerning the origin and function of the branchial appendages in this species. Branchiae 4 and 5 may not be homologous with B1–B3 because the latter arise from the branchial membrane and are clavate-cirriform in shape, whereas B4 and B5 arise posterior to the branchial membrane and B4, at least, is foliaceous. None of the material had B5 present and the shape of this structure is unknown. However, as flabelligerids may have 2 different types of branchial appendages (e.g., *Diplocirrus* species), for the present all 5 pairs are tentatively considered to be branchiae. A phylogenetic revision of the family may serve to clarify this point.

Acknowledgments

This paper was completed using the Postdoctoral Fellowship of CJG at the National Museum of Natural History, Smithsonian Institution.

Literature Cited

Chamberlin, R. V. 1919. The Annelida Polychaeta. Pp. 1–514 + pls. 1–80 *in* Reports on the scientific results of the expeditions of the U.S. Fish Commission Steamer 'Albatross', 1891, 1899–1900 and 1904–1905.—Memoirs of the Museum of Comparative Zoology, Harvard 48.

Fauchald, K. 1972. Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean.—Allan Hancock Monographs in Marine Biology 7:1–575.

———. 1977. The polychaete worms. Definitions and keys to the orders, families and genera. Natural History Museum of Los Angeles County, Los Angeles, 188 pp.

George, J. D., & G. Hartmann-Schröder. 1985. Polychaetes: British Amphinomida, Spintherida & Eunicida. Keys and notes for the identification of the species. Pp. 1–221 *in* D. M. Kermack & R. S. K. Barnes, eds., Synopses of the British fauna No. 32. E. J. Brill, Dr. W. Backhuys, Leiden.

Haase, P. 1915. Boreale und arktische Chloraemiden. Wissenschaftliche Meeresuntersuchungen Abteilung Kiel 17:169–228 [not seen].

Hartman, O. 1967. Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic Seas.—Allan Hancock Monographs in Marine Biology 2:1–387.

———. 1978. Polychaeta from the Weddell Sea quadrant, Antarctica. Paper 4. Pp. 125–223 *in* D. L. Pawson, ed., Biology of the Antarctic seas VI. Antarctic Research Series 26.

McIntosh, W. C. 1885. Report on the Annelida Polychaeta collected by H.M.S. 'Challenger' during the years 1873–1876.—Challenger Reports 12: 1–554.

Saint-Joseph, M. le Baron de. 1894. Les Annélides Polychètes des côtes de Dinard. Pt 3.—Annales des Sciences Naturelles. Zoologie et Paléontologie 7(17):1–395.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 688–713

POLYNOIDS COMMENSAL WITH GORGONIAN AND STYLASTERID CORALS, WITH A NEW GENUS, NEW COMBINATIONS, AND NEW SPECIES (POLYCHAETA: POLYNOIDAE: POLYNOINAE)

Marian H. Pettibone

Abstract.—Some commensal polynoids, living in close association with gorgonian and stylasterid corals, are referred to a new genus, *Gorgoniapolynoe,* including *Polynoe caeciliae* Fauvel, *Harmothoe corralophila* Day, *Polynoe uschakovi* Britayev, and five new species (*G. bayeri, G. cairnsi, G. galapagensis, G. muzikae, G. pelagica*). The polynoids invade the corals, resulting in galls and tunnels for the passage of the worms. The anterior few elytral pairs of the polynoids are modified. An additional bathypelagic polynoid from off Bermuda, showing the same type of modified elytra, is also included as a new species in the genus.

Many polynoid species are found living in close association with corals. Among them are some species that invade gorgonian and stylasterid corals, causing the latter to grow around them, and forming galls with open tunnels on their sides for passage of the polynoids. In this group of polynoids, the anterior one to three pairs of elytra are modified, forming translucent chitinous areas with scattered microtubercles and micropapillae. This condition was shown by Day (1960:278, fig. 2a) for *Harmothoe corralophila,* associated with the stylasterid *Allopora bithalamus,* and by Britayev (1981:819, fig. 1:1–9) for *Polynoe uschakovi,* associated with the gorgonian *Callogorgia* sp. The two polynoid species are referred herein to the new genus *Gorgoniapolynoe.* Also included in the new genus are *Polynoe caeciliae* Fauvel, 1913 (which is associated with the gorgonian *Corallium johnsoni*), and five new species. A small bathypelagic polynoid from off Bermuda, possibly a juvenile, is also placed here, based on the same unique type of anterior elytra as found in the species referred to the new genus.

The polynoid commensals were removed from their gorgonian and stylasterid hosts by Frederick M. Bayer, Katherine M. Muzik, Stephen D. Cairns, Lauren Mullineaux, and Helmut Zibrowius (for Gesa Hartmann-Schröder). In addition to the USNM collections in the Smithsonian Institution, the specimens examined are deposited in the British Museum of Natural History, London (BMNH); the Muséum National d'Histoire Naturelle, Paris (MNHNP); the Musée de Monaco, Monaco-Ville (MOM); the Zoologisches Staatsmuseum, Hamburg (ZMH); the Zoological Museum State University, Moscow (ZMSUM); and the Zoological Institute Academy of Sciences, Leningrad (ZIASL).

Family Polynoidae Kinberg, 1856
Subfamily Polynoinae Kinberg, 1856
Gorgoniapolynoe, new genus

Type species.—*Gorgoniapolynoe bayeri,* new species. Gender: feminine.

Type locality.—Philippine Islands, with gorgonian *Narella clavata* (Versluys).

Diagnosis.—Segments 33–63. Elytra and elytrophores 15 pairs, on segments 2, 4, 5,

7, alternate segments to 23, 26, 29, and 32. Anterior 1–3 pairs of elytra modified, with amber-colored, translucent, chitinous central area furnished with microtubercles and micropapillae; following elytra smooth, without tubercles. Dorsal cirri on non-elytrigerous segments, with cirrophores and long distal styles; dorsal tubercles in line with elytrophores. Prostomium bilobed, with lobes rounded to subtriangular, with or without small cephalic peaks; median antenna with ceratophore in anterior notch, with long distal style; short lateral antennae with distinct ceratophores inserted ventrally, removed from median antenna; palps stout, tapered; 2 pairs of eyes. First segment not distinct dorsally; tentaculophores lateral to prostomium, usually achaetous, with 2 pairs of dorsal and ventral tentacular cirri. Second or buccal segment without nuchal fold, with first pair of elytrophores, biramous parapodia and long ventral buccal cirri, lateral to mouth. Eversible pharynx with 9 pairs of border papillae and 2 pairs of jaws. Parapodia biramous, with notopodia subconical, smaller and shorter than neuropodia; neuropodia with presetal acicular lobe diagonally truncate, with thick, digitiform or bulbous supraacicular process; postsetal lobe shorter, rounded. Notosetae few (0–7), extending only slightly beyond notopodia, smooth, acicular, about as stout as neurosetae. Neurosetae with faint spinose rows, all or mostly all with bifid tips. Ventral cirri extending to about tips of neuropodia. Prominent thickened glandular areas on bases of ventral cirri, beginning about segment 11–18. Commensal with gorgonian and stylasterid hydrocorals, forming mucous tubes and modifying the host, forming tunnels.

Exceptions to the above diagnosis include the following: for *G. corralophila,* notosetae long and numerous, with spinose rows; neurosetae with prominent spinose rows; for *G. pelagica,* bathypelagic, not associated with hydrocorals, 15 segments, 12 pairs of elytra, notosetae long, with spinose rows, forming radiating bundle. The two species are included in the genus based on the unique modified anterior elytra.

Etymology.—The genus name is based on the association of polynoid worms with some gorgonian corals.

1. First pair of elytra modified (Figs. 5A, B, 7A, B, 9A, C, 12A, B, 14A, B, 16A, C; Britayev 1981, fig. 1:5, 7) 2
– First and 2nd pairs of elytra modified (Figs. 1A, C, D, 3A–C). Notosetae few, short, acicular (Figs. 2B, C, E, F, 4C, D, F) 7
– First, 2nd, and 3rd pairs of elytra modified (Fig. 15A, B; Day 1960, fig. 2a). Notosetae numerous, long, with spinose rows (Fig. 15D–F). Prostomial lobes wide, subtriangular, with small peaks (Fig. 15A). Commensal with stylasterid *Allopora bithalamus* .... *G. corralophila* (Day), new combination
2. Body with 12 pairs of elytra and 25 segments. Notosetae numerous, long, with spinose rows (Fig. 16E–G). Prostomial lobes rounded, without peaks (Fig. 16A). Bathypelagic ..... *G. pelagica,* new species
– Body with 15 pairs of elytra and 33–63 segments. Notosetae few, short, smooth, acicular (Figs. 6C, D, 8C, D, 10A–C, E, F, 14E–G, I). Commensal with gorgonian and stylasterid corals 3
3. Chitinous area of modified elytra large, with narrow, clear border (Figs. 5A, B, 7A, B) 4
– Chitinous area of modified elytra small, with wide, clear, medial border (Figs. 9A, C, 12A, B, 14A, B; Britayev 1981, fig. 1:5) 5
4. Elytral chitinous area with crescent-shaped microtubercles and circular micropapillae (Fig. 5B). Prostomial lobes wide, subtriangular, without

cephalic peaks (Fig. 5A). Commensal with gorgonians, Primnoidae: *Candidella helminthophora,* Corallidae: *Corallium* sp., and Acanthogorgiidae: *Acanthogorgia* sp. .... *G. muzikae,* new species

– Elytral chitinous area with oval microtubercles and globular micropapillae (Fig. 7B). Prostomial lobes rounded, with small cephalic peaks (Fig. 7A). Commensal with gorgonian, Primnoidae: *Narella ambigua* ..... *G. galapagensis,* new species

5. Elytral chitinous area with conical and round microtubercles and cylindrical micropapillae (Britayev 1981, fig. 1:7a–e). Commensal with gorgonian, Primnoidae: *Callogorgia* sp. ..... *G. uschakovi* (Britayev), new combination

– Elytral chitinous area with round microtubercles and elongate, globular micropapillae (Figs. 9C, 12B) 6

6. Prostomial lobes truncate, without peaks (Fig. 9B). Commensal with gorgonians, Corallidae: *Corallium imperiale* .... *G. guadalupensis,* new species

– Prostomial lobes rounded, without peaks (Figs. 12A, 14A). Commensal with gorgonians, Corallidae: *Corallium johnsoni, C. niobe, C. tricolor*; Primnoidae: *Candidella imbricata*; Acanthogorgiidae: *Acanthogorgia aspera* ..... *G. caeciliae* (Fauvel), new combination

7. Chitinous area of modified elytra with low microtubercles and globular micropapillae (Fig. 1C). Neurosetae with short, stout secondary tooth (Fig. 2D). Prostomial lobes rounded, without peaks (Fig. 1B). Commensal with gorgonian, Primnoidae: *Narella clavata* .... *G. bayeri,* new species

– Chitinous area of modified elytra with conical microtubercles and cylindrical micropapillae (Fig. 3B). Neurosetae with long, delicate secondary tooth (Fig. 4G). Prostomial lobes wide, subtriangular, without peaks (Fig. 3A). Commensal with stylasterid *Allopora eguchii* .... *G. cairnsi,* new species

Gorgoniapolynoe bayeri, new species
Figs. 1, 2

Material examined.—North Pacific Ocean: Philippine Islands, North Mindanao, Tagolo Light, 8°47′N, 123°35′E, 294 m, *Albatross* sta 5543, 20 Aug 1909, on gorgonian *Narella clavata,* removed by F. M. Bayer, holotype (USNM 80080), paratype (USNM 80081).

Description.—Holotype incomplete posteriorly, 7 mm long, 2 mm wide including setae, 35 segments; complete paratype 10 mm long, 2 mm wide, 43 segments. Body elongate, flattened, tapering posteriorly. First 2 pairs of elytra modified: central part amber-colored, chitinous, translucent, with scattered low microtubercles and globular micropapillae; thicker chitinous area on posterior and lateral sides and narrow light border (Fig. 1A, C, D). Following elytra thin, transparent, without tubercles or papillae, denser around place of attachment; elytra becoming smaller posteriorly (Fig. 1E, F). Dorsal cirri with large cylindrical cirrophores on posterior sides of notopodia; styles long, tapering distally, extending far beyond neurosetae, with scattered clavate micropapillae; dorsal tubercles nodular (Figs. 1B, 2A, F).

Prostomium bilobed, rounded anteriorly, without cephalic peaks; ceratophore of median antenna in anterior notch, with style long, tapered, extending far beyond palps and extended pharynx; lateral antennae with distinct ceratophores inserted on lateroventral part of prostomium, some distance from ceratophore of median antenna, with short, subulate styles; palps stout, tapered; 2 pairs of eyes moderate in size, anterior pair in region of greatest width, posterior pair pos-

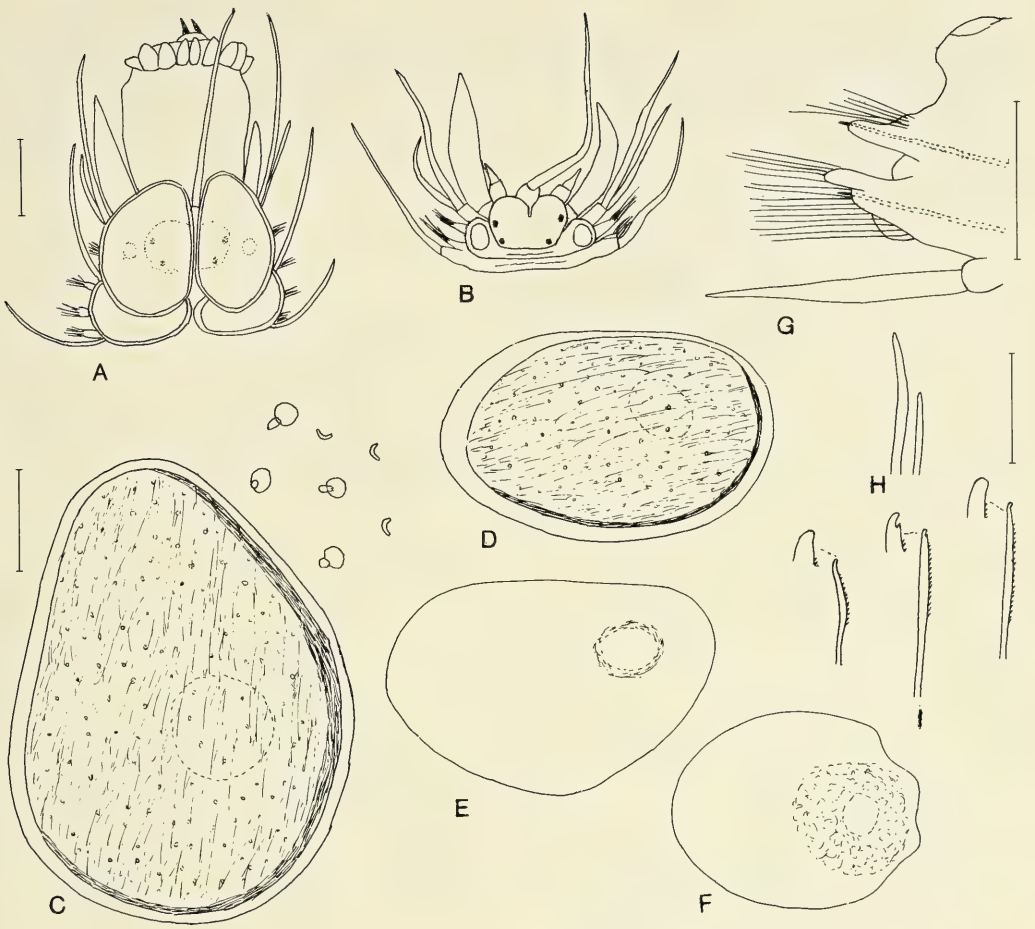


Fig. 1. *Gorgoniapolynoe bayeri,* holotype (USNM 80081): A, Dorsal view of anterior end, pharynx fully extended; B, Same, elytra removed, pharynx not shown; C, Right 1st elytron from segment 2, with detail of micropapillae and microtubercles; D, Right 2nd elytron from segment 4; E, Right 3rd elytron from segment 5; F, Right 6th elytron from segment 11; G, Right elytrigerous parapodium from segment 2, anterior view, acicula dotted; H, Notosetae from same; I, Lower, middle and upper neurosetae from same, with detail of tips. Scales = 0.5 mm for A, B; 0.2 mm for C–F; 0.2 mm for G; 0.1 mm for H, I.

terolateral (Fig. 1A, B). Tentaculophores lateral to prostomium, achaetous, with 2 pairs of tentacular cirri, dorsal pair slightly shorter than median antenna and longer than ventral pair (Fig. 1B). Segment 2 without nuchal fold, with large elytrophores, biramous parapodia, and ventral buccal cirri longer than following ventral cirri, similar to tentacular cirri (Fig. 1B, G). Notosetae few (7), smooth, with pointed tips (Fig. 1H); neurosetae slender, finely spinose, upper and lower ones with blunt tips, middle ones with notched or bifid tips (Fig. 1I). Extended pharynx with 9 dorsal and 9 ventral border papillae and 2 pairs of chitinous jaws (Fig. 1A).

Biramous parapodia with conical notopodium, smaller and slightly shorter than neuropodium; neuropodium with longer, subconical presetal acicular lobe with thick, short, digitiform supraacicular process and shorter, subconical postsetal lobe (Fig. 2A, B). Notosetae relatively few (7 on 2nd, 6–4 on 10th–12th, 2 on mid-body), extending

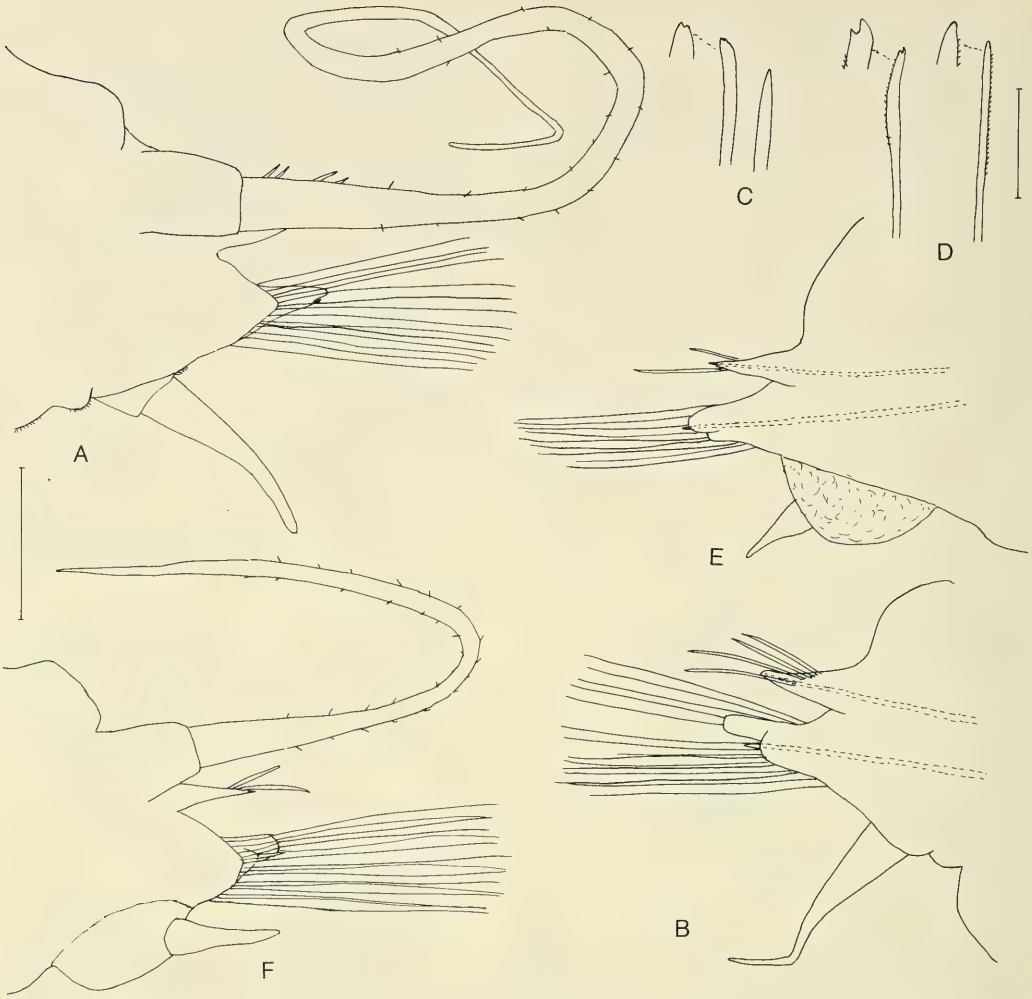


Fig. 2. *Gorgoniapolynoe bayeri,* holotype (USNM 80081): A, Right cirrigerous parapodium from segment 10, posterior view; B, Right elytrigerous parapodium from segment 11, anterior view, acicula dotted; C, Notosetae from same, with detail of tip; D, Middle and upper neurosetae from same, with detail of tips; E, Right middle elytrigerous parapodium, anterior view, acicula dotted; F, Right middle cirrigerous parapodium, posterior view. Scales = 0.2 mm for A, B, E, F; 0.1 mm for C, D.

beyond tip of neuropodium, slightly stouter than neurosetae, smooth, with tips pointed, some with slightly notched tips (Fig. 2C). Supraacicular neurosetae slightly more slender, with longer, faint spinose regions, and entire or slightly notched tips; subacicular neurosetae with shorter spinose regions and bifid tips (Fig. 2D). Ventral cirri short, tapering, extending to about tips of neuropodia (Fig. 2A, B). Enlarged glandular areas on bases of ventral cirri, beginning about segment 18 (Fig. 2E, F). Small nephridial papillae beginning on segment 6. Pygidium with pair of long anal cirri.

Etymology.—The species is named for Frederick M. Bayer, who removed the polynoid and identified the gorgonian host.

Biology.—*Gorgoniapolynoe bayeri* was collected on the gorgonian *Narella clavata* (Versluys) (Gorgonacea: Primnoidae), where

the enlarged basal scales of the polyps arch over, overlap, and produce tunnels for the passage of the worm.

Distribution.—North Pacific Ocean, Philippine Islands, in 294 meters.

Gorgoniapolynoe cairnsi, new species
Figs. 3, 4

Material examined.—Southern Ocean: off Auckland Islands, 51°00′S, 162°01′E, 333–371 m, *Eltanin* sta 1411, 8 Feb 1965, in calcareous stem of stylasterid hydrocoral *Allopora eguchii,* holotype (USNM 80082), 3 paratypes (USNM 80084), young paratype (USNM 80083), all removed by S. Cairns.

Description.—Holotype 12 mm long, 4 mm wide, 42 segments; paratypes 15 mm long, 4 mm wide, 42 and 45 segments; young paratype 11 mm long, 4 mm wide, 36 segments. Body elongate, linear, flattened dorsoventrally, tapering slightly anteriorly and more so posteriorly. First pair of elytra covering prostomium, rest leaving middorsum uncovered. First 2 pairs of elytra modified: central area amber-colored, chitinous, transparent, with low conical microtubercles and cylindrical micropapillae; surrounding area smooth, except for few micropapillae (Fig. 3A–C). Following elytra smooth, denser around place of attachment to elytrophores, with some scattered micropapillae (Fig. 3C, D). Dorsal cirri with cylindrical cirrophores and styles extending far beyond setae, anterior ones mostly thick, bulbous basally, with few micropapillae, posterior ones long, slender, cylindrical; dorsal tubercles inflated, nodular (Fig. 4A, E).

Bilobed prostomium with anterior lobes wide, subtriangular, without distinct peaks; ceratophore of median antenna in anterior notch, style longer than palps; ceratophores of lateral antennae inserted lateroventrally, some distance from ceratophore of median antenna, with styles short, subulate; palps stout, tapered; 2 pairs of rather large eyes, anterior pair in region of greatest width, larger than posterolateral pair (Fig. 3A). Tentaculophores lateral to prostomium, each with single aciculum, 0–1 setae, and pair of long, tapering tentacular cirri, similar to median antenna; dorsal one longer than ventral one (Fig. 3A, F). Segment 2 with first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri; notosetae lacking; neurosetae slender, spinose, with bulbous tips and slender secondary tooth (Fig. 3A, G, H).

Biramous parapodia with smaller notopodium, short, subconical; larger neuropodium with subconical presetal acicular lobe with thick supraacicular process; postsetal lobe shorter, subconical to rounded (Fig. 4A, C–E). Notosetae few (0 on segments 2 and 3, 2–5 on following segments), smooth, acicular (Fig. 4F). Upper neurosetae with long spinose regions, and delicate secondary tooth; lower neurosetae with short spinose regions, mostly with delicate secondary tooth (Fig. 4B, G). Ventral cirri short, subulate, rather thick basally (Fig. 4A, C–E). Nephridial papillae small, directed dorsally, beginning on segment 6. Pygidium with pair of anal cirri.

Young paratype (USNM 80083) of 11 mm long and 26 segments showing some differences from above description: first pair of elytra missing, 2nd and 3rd pairs with chitinous areas; prostomium with small peaks and eyes slightly smaller; notosetae 5–7 in number, with 7–8 spinose rows, instead of smooth.

Etymology.—The species is named for Stephen D. Cairns, whose studies on the stylasterid hydrocorals have disclosed and contributed numerous polynoid commensals, including the present ones.

Biology.—*Gorgoniapolynoe cairnsi* was found in the calcareous stems of *Allopora eguchii* Boschma (Stylasterina, Stylasteridae), identified by S. Cairns and reported by Cairns (1983:145) as an undescribed genus and species.

Fig. 3. *Gorgoniapolynoe cairnsi,* holotype (USNM 80082): A, Dorsal view of anterior end, pharynx partially extended, only right 2nd elytron shown; left palp small, regenerating; B, Right 1st elytron from segment 2, with detail of microtubercles and micropapillae; C, Right 2nd elytron from segment 4; D, Right 3rd elytron from segment 5; E, Left 15th elytron from segment 32; F, Right tentaculophore from segment 1, dorsal tentacular cirrus broken off, aciculum dotted; G, Right elytrigerous parapodium from segment 2, anterior view, acicula dotted; H, Neuroseta from same, with detail of tip. Scales = 0.5 mm for A; 0.2 mm for B–E; 0.2 mm for F, G; 0.1 mm for H.

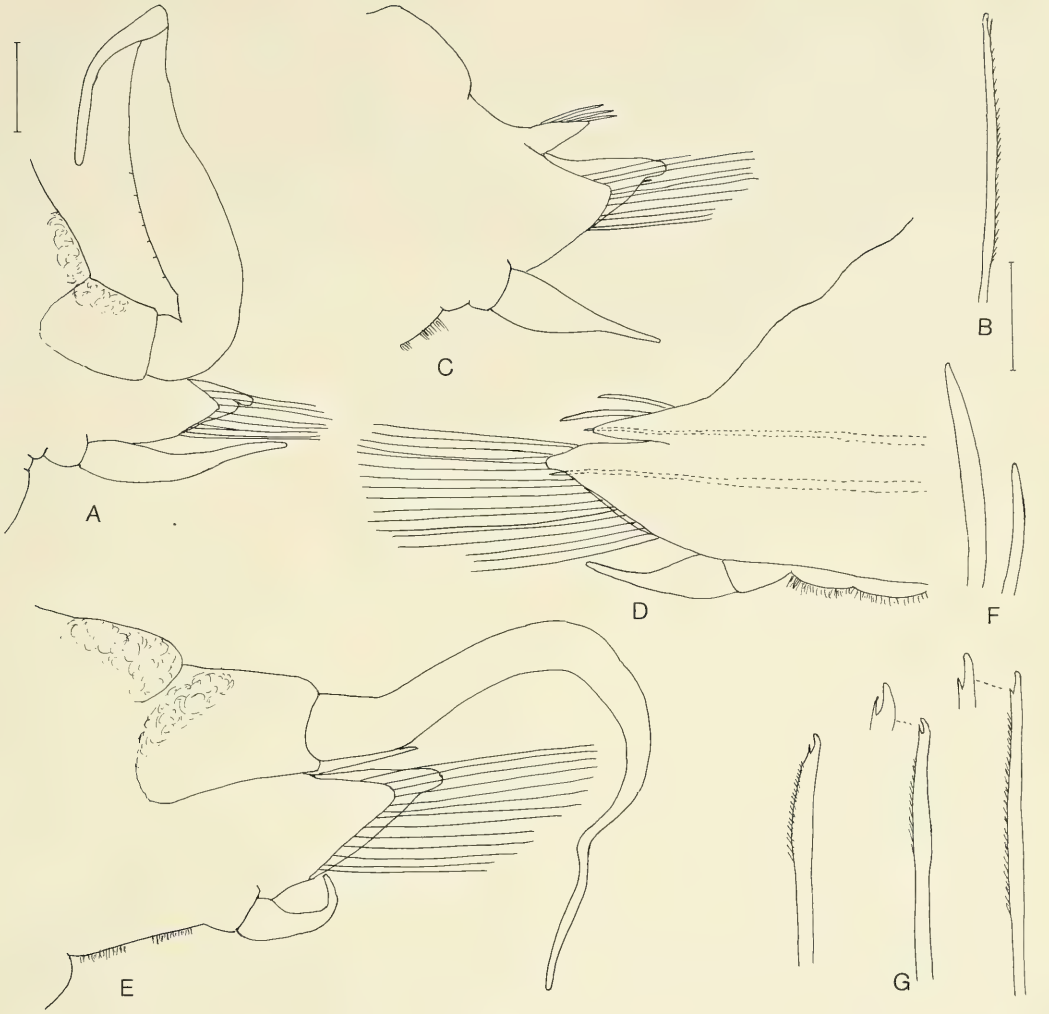


Fig. 4. *Gorgoniapolynoe cairnsi,* holotype (USNM 80082): A, Right cirrigerous parapodium from segment 3, posterior view; B, Neuroseta from same; C, Right elytrigerous parapodium from segment 5, posterior view; D, Right elytrigerous parapodium from segment 23, anterior view, acicula dotted; E, Right cirrigerous parapodium from segment 24, posterior view; F, Notosetae from same; G, Lower, middle and upper neurosetae from same, with detail of tips. Scales = 0.2 mm for A, C–E; 0.1 mm for B, F, G.

Distribution.—Antarctic, off Auckland Islands, in 333–371 meters.

Gorgoniapolynoe muzikae, new species
Figs. 5, 6

Material examined.—North Pacific Ocean: Hawaiian Islands, French Frigate Shoals, 23°30′N, 164°41′W, 29–311 m, *Albatross* sta 3975, 31 May 1902, on *Candidella helminthophora,* removed by F. M. Bayer, 8 paratypes (USNM 80095). Off Modu Manu (Bird Island), 22°27′N, 160°40′W, 523–1038 m, *Albatross* sta 4156, 6 Aug 1902, on *Acanthogorgia* sp., removed by K. M. Muzik, holotype (USNM 80093), 2 paratypes (USNM 80094). Kaena Point, Oahu, 377 m, dive 9, 18 Dec 1973, R. Grigg,

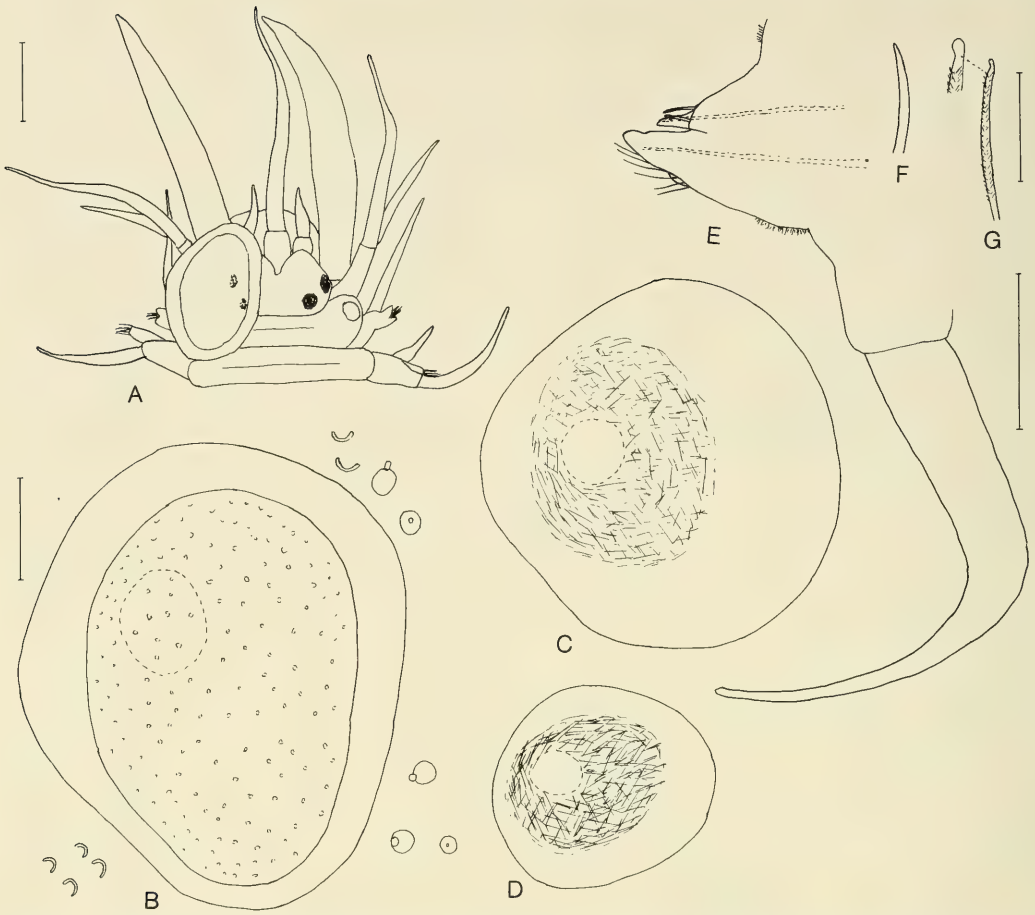


Fig. 5. *Gorgoniapolynoe muzikae*, holotype (USNM 80093): A, Dorsal view of anterior end, pharynx partially extended, right first elytron removed; B, Left 1st elytron, with detail of microtubercles and micropapillae; C, Left middle elytron; D, Left posterior elytron; E, Right elytrigerous parapodium from segment 2, anterior view, acicula dotted, elytrophore not shown; F, Notoseta from same; G, Neuroseta from same, with detail of tip. Scales = 0.5 mm for A; 0.2 mm for B–D; 0.2 mm for E; 0.1 mm for F, G.

collector, with *Corallium* sp., removed by K. M. Muzik, 9 paratypes (USNM 80096).

Description.—Holotype on *Acanthogorgia* 15 mm long, 2 mm wide with setae, 48 segments; larger paratype 18 mm long, 3 mm wide, 52 segments; young paratype 5 mm long, 2 mm wide, 25 segments. Paratypes on *Candidella* 6–8 mm long, 2 mm wide, 33–40 segments. Paratypes on *Corallium* 8–20 mm long, 2–3 mm wide, 43–62 segments.

Body slender, linear, flattened dorsoventrally, tapering posteriorly. First pair of elytra large, nearly covering prostomium, modified: central part chitinous, yellowish amber-colored, translucent, with scattered crescent-shaped microtubercles and circular micropapillae with stems penetrating chitinous layer; outer rim thicker, dense, non-chitinous (Fig. 5A, B). Following elytra smaller, attached eccentrically, smooth, transparent, with denser central area around place of attachment (Fig. 5C, D). Dorsal cirri with cylindrical cirrophores posterodorsal to notopodia, with long styles extending far beyond neurosetae, with scat-

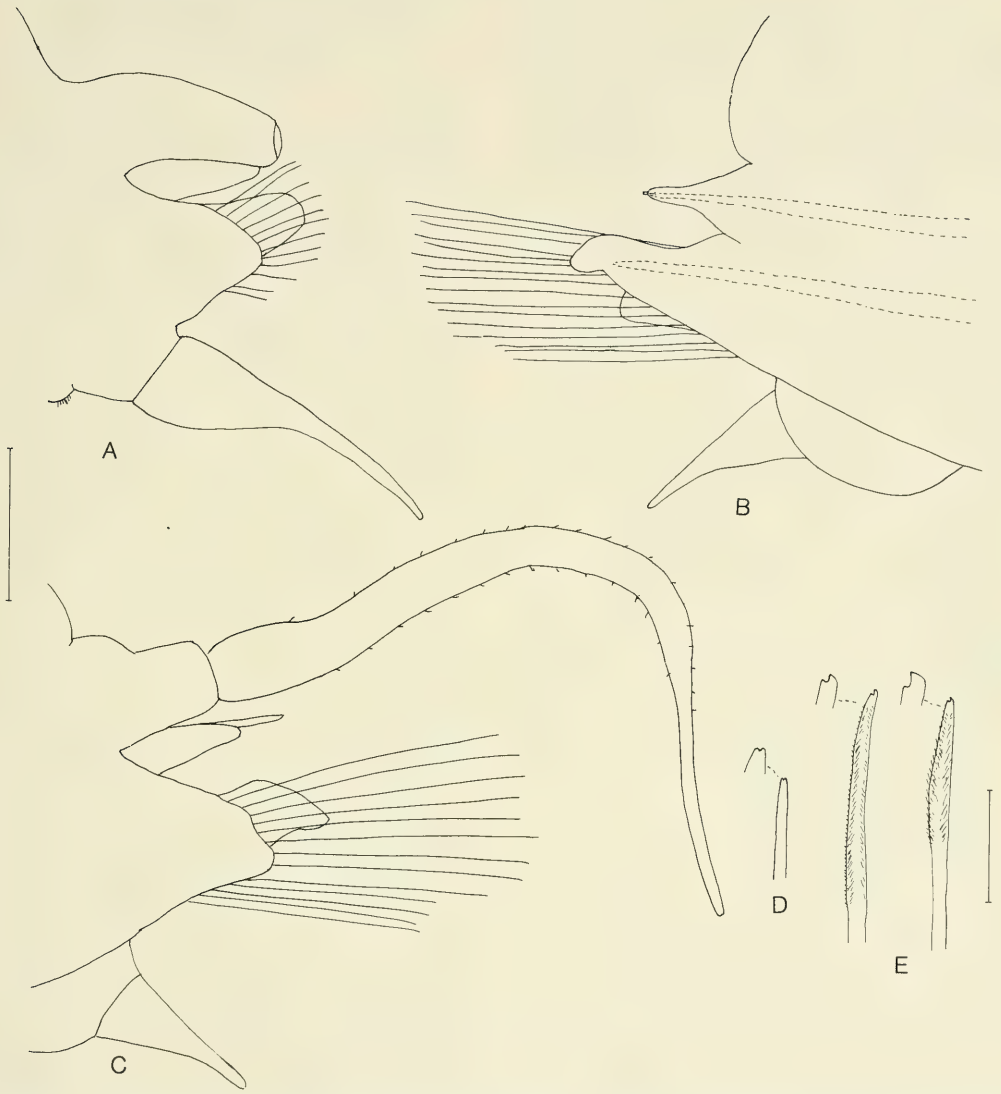


Fig. 6. *Gorgoniapolynoe muzikae,* holotype (USNM 80093): A, Right cirrigerous parapodium from segment 3, posterior view, style of dorsal cirrus missing; B, Right middle elytrigerous parapodium, anterior view, acicula dotted; C, Right middle cirrigerous parapodium, posterior view; D, Notoseta from same, with detail of tip; E, Upper and middle neurosetae, with detail of tips. Scales = 0.2 mm for A–C; 0.1 mm for D, E.

tered clavate micropapillae, and filamentous tip; dorsal tubercles bulbous (Figs. 5A, 6A, C).

Bilobed prostomium with anterior lobes subtriangular, without distinct cephalic peaks; ceratophore of median antenna in anterior notch, style long, with filamentous tip; lateral antenna with ceratophores inserted lateroventrally, removed from median antenna, with styles short, subulate; palps stout, tapered, about as long as median antenna; eyes rather large, anterior pair in region of greatest width, slightly larger than posterodorsal pair (Fig. 5A). Tentaculophores lateral to prostomium, achaetous; dorsal and ventral tentacular cirri similar to

but shorter than median antenna (Fig. 5A). Segment 2 with first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri (Fig. 5A, E); notosetae few, smooth, acicular (Fig. 5F); neurosetae slender, with long spinose region and knobbed tips (Fig. 5G). Pharynx with 9 dorsal and 9 ventral border papillae and 2 pairs of light amber-colored jaws.

Biramous parapodia with notopodium subconical, smaller and shorter than neuropodium; larger neuropodium subconical, diagonally truncate, presetal acicular lobe with thick, digitiform supraacicular process; postsetal lobe shorter, rounded (Fig. 6A–C). Notosetae few (0–4), extending only slightly beyond tips of notopodia, smooth, acicular, with tips pointed or minutely notched (Fig. 6D). Neurosetae relatively few (about 12), upper few with long spinose regions, middle and lower ones with short spinose regions, all with bifid hooked tips (Fig. 6E). Ventral cirri rather large, subulate; prominent bulbous areas on bases of ventral cirri, beginning about segment 11 (Fig. 6B, C). Nephridial papillae small, beginning on segment 6. Pygidium with pair of anal cirri.

Etymology.—The species is named for Katherine M. Muzik, who removed the polynoids and identified the gorgonian hosts of the holotype and some of the paratypes.

Biology.—All the host species produce tunnels for the passage of the polynoids, including Primnoidae: *Candidella helminthophora* (Nutting), identified by F. M. Bayer; Acanthogorgiidae: *Acanthogorgia* sp. and Corallidae: *Corallium* sp., identified by K. M. Muzik. In the primnoid *Candidella,* the enlarged basal scales arch over, overlap, and produce tunnels. In *Corallium* and *Acanthogorgia,* the tunnels are formed by lateral coenenchymal expansions that arch over the branch, often meeting and fusing along the midline of the branch. In *Corallium,* the axis may also be expanded (more or less), within the coenenchymal flaps.

Distribution.—North Pacific Ocean, Hawaiian Islands, in 29–1038 meters.

Gorgoniapolynoe galapagensis,
new species
Figs. 7, 8

Material examined.—Eastern Central Pacific Ocean: Galapagos Islands, 0°29′S, 89°54′W, 417 m, *Albatross* sta 2818, 15 Apr 1885, with gorgonian *Narella ambigua,* holotype (USNM 80085), paratype (USNM 80086), 5 paratypes (USNM 80087), all removed by F. M. Bayer.

Description.—Holotype 17 mm long, 3 mm wide with setae, 49 segments; paratype 13 mm long, 2.5 mm wide 49 segments. Body linear, flattened, tapering posteriorly. First pair of elytra large, elongate-oval, modified: chitinous central part with scattered microtubercles and globular papillae, and enclosed in thickened, dense, colorless part (Fig. 7A, B); following elytra smaller, oval, transparent, denser around place of attachment to elytrophore (Fig. 7A, C–E). Dorsal cirri with cylindrical cirrophores and styles extending far beyond neurosetae; dorsal tubercles nodular (Figs. 7A, 8A, B).

Bilobed prostomium with small cephalic peaks; ceratophore of median antenna in anterior notch; style long, with filamentous tip; ceratophores of lateral antennae inserted lateroventrally, removed from median antenna, with styles short, subulate; palps stout, tapered, shorter than median antenna; eyes rather large, anterior pair in region of greatest width of prostomium, slightly larger than posterior pair (Fig. 7A). Tentaculophores lateral to prostomium, achaetous; dorsal and ventral tentacular cirri similar to median antenna, dorsal ones slightly longer than ventral ones (Fig. 7A). Segment 2 with first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri (Fig. 7A, F); notosetae few (2), acicular (Fig. 7G); neurosetae spinose, upper ones with slightly curved, entire, bare tips, lower ones with clubbed tips (Fig. 7H).

Biramous parapodia with smaller, conical notopodia, extending almost as far as larger neuropodia; neuropodia with diagonally

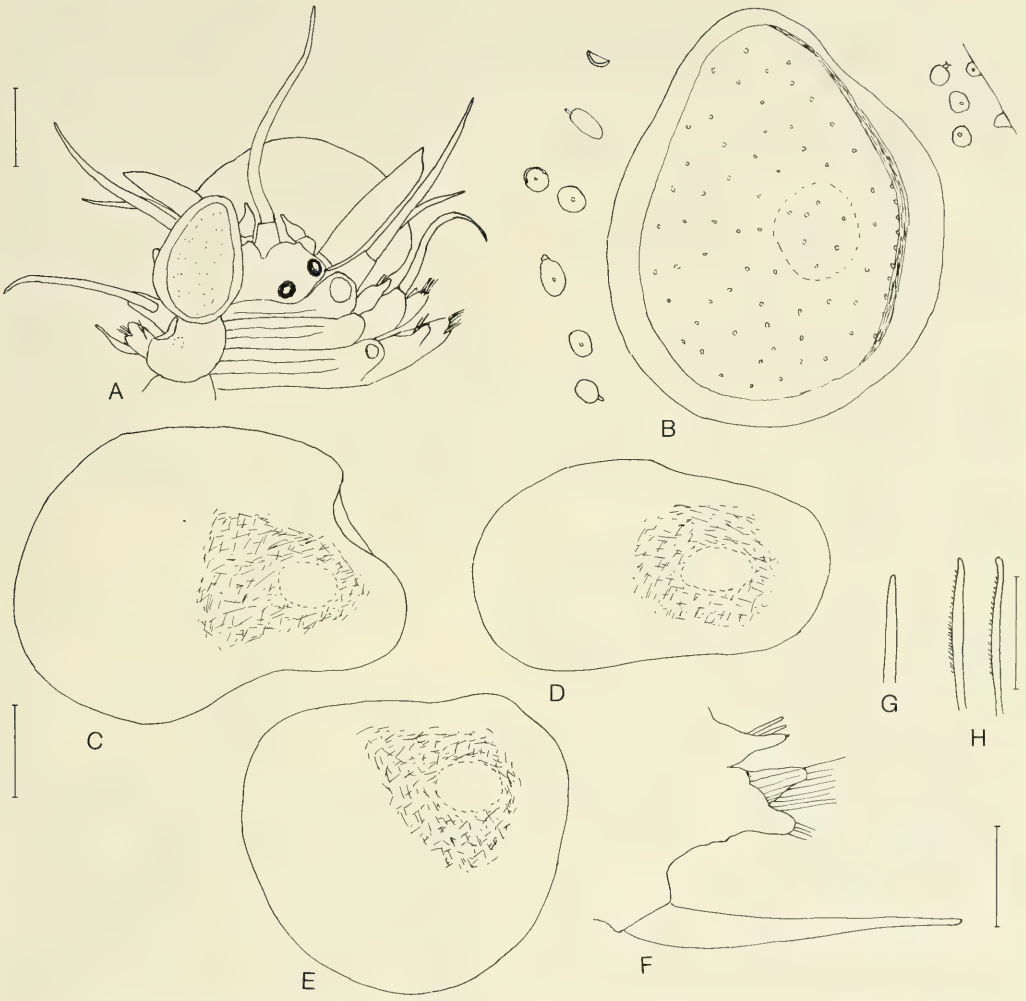


Fig. 7. *Gorgoniapolynoe galapagensis,* holotype (USNM 80085): A, Dorsal view of anterior end, pharynx partially extended, right elytra removed; B, Right 1st elytron from segment 2, with detail of microtubercles and micropapillae; C, Right 2nd elytron from segment 4; D, Right 3rd elytron from segment 5; E, Right 5th elytron from segment 9; F, Right elytrigerous parapodium from segment 2, posterior view; G, Notoseta from same; H, Upper and lower neurosetae from same. Scales = 0.5 mm for A; 0.2 mm for B–E; 0.2 mm for F; 0.1 mm for G, H.

truncate presetal acicular lobe, with thick, digitiform supraacicular process and shorter, truncate postsetal lobe, longer on lower part (Figs. 7F, 8A–C, F, G). Notosetae few (0–2), short, acicular (Fig. 8D). Neurosetae with faint spinose rows, upper ones with slightly longer spinose regions and entire tips; middle ones with distinct or slight indication of secondary tooth; lower ones with entire tips (Fig. 8E). Ventral cirri enlarged basally, extending to about tips of neuropodia (Fig. 8A–C); beginning about segment 14, enlarged bulbous region below ventral cirri (Fig. 8F, G).

Etymology.—The species is named for the collecting site, the Galapagos Islands.

Biology.—*Gorgoniapolynoe galapagensis* was found with *Narella ambigua* (Studer), Gorgonacea: Primnoidae, where the enlarged basal scales of the polyps arch over,

overlap, and produce tunnels for the passage of the polynoids. The gorgonians were identified by F. M. Bayer.

Distribution.—Eastern Central Pacific Ocean, Galapagos Islands, in 417 meters.

Gorgoniapolynoe uschakovi
(Britayev, 1981), new combination

Polynoe uschakovi Britayev, 1981:819, fig. 1:1–9 (part).

Material examined.—Central Pacific Ocean: Vityaz Ridge, 18°02′N, 173°35′E, 1360–1500 m, R/V *Dmitriy Mendeleev* sta 1722, 2 Sep 1978, 1360–1500 m, with gorgonian *Callogorgia* sp., paratype of *Polynoe uschakovi* (ZIASL 2/44391).

Remarks.—The species was based on specimens from two areas in the Central Pacific: the Vityaz Ridge, commensal with the gorgonian *Callogorgia* sp. (including the holotype and 7 paratypes) and the Guyot Ridge, commensal with the pink coral *Corallium* sp. (as *Allopora* sp.), including 22 paratypes. As indicated by Britayev, the two groups differed in some respects. The description and figures of the holotype from the Vityaz Ridge (fig. 1:1–3a, c, 4–8) are referred herein to *Gorgoniapolynoe uschakovi*; the discussion of the differences and figures of the paratypes from the Guyot Ridge (fig. 1:3b, 9) are referred to *G. guadalupensis.*

The paratype examined is complete, 9 mm long, 2 mm wide with parapodia, and 42 segments, with the pharynx extended, compared with the holotype stated as being 16 mm long, 1.3 mm wide, and 43 segments. The characteristic first pair of elytra are now missing. As originally described, they are modified, the chitinous part with conical and oval microtubercles and cylindrical micropapillae, and with a large non-chitinous part on the inner side (fig. 1:5, 7a–e). The bilobed prostomium has the anterior lobes wide, subtriangular, without peaks, 2 pairs of large eyes, median antenna with the ceratophore in the anterior notch, with long style, and short lateral antennae with prominent ceratophores inserted ventrally (fig. 1:1). The tentaculophores lateral to the prostomium have long dorsal and ventral tentacular cirri, similar to the median antenna. The extended pharynx has 9 pairs of border papillae and 2 pairs of jaws. The biramous parapodia have small notopodia with few, smooth, acicular notosetae (usually 2, 1–7, according to Britayev, fig. 1:3a); the larger neuropodia end in a presetal acicular process (fig. 1:2); the neurosetae have faint, oblique striations or toothed scales and bifid notched tips (fig. 1:3c, 4). They are found on branches of the gorgonian along the main stem, partly hidden by the sclerites of the polyps (fig. 1:8).

Gorgoniapolynoe guadalupensis,
new species
Figs. 9–11

Polynoe uschakovi Britayev, 1981:819 (part, fig. 1:3b, 9; not holotype).

Material examined.—Eastern Central Pacific Ocean: SW of Guadalupe Island off west coast of Baja California, 27°23′N, 119°19′W, 1000–2000 m, Robert H. Parker Scripps Pelagic Studies Cruise, 24 Apr 1954, on holotype of *Corallium imperiale,* holotype (USNM 80088); 3 paratypes (USNM 80089), removed by F. M. Bayer; 32 specimens (USNM 133354), removed by M. Pettibone. Fieberling Guyot seamount, 32°23′N, 127°47′W, about 600 m, Aug 1989, L. Mullineaux, collector, in tube of pink coral *Corallium imperiale,* identified by F. M. Bayer, 12 specimens (USNM 133355). Guyot Ridge on Markus Nekar Chain, 13°27′N, 173°27′W, 1220–1300 m, R/V *Vityaz* sta 3789, 24 Nov 1957, with pink coral *Corallium imperiale,* 2 paratypes of *Polynoe uschakovi* (USNM 134352, from ZMSUM).

Description.—Holotype 17 mm long, 2.5 mm wide with setae, 55 segments; 3 paratypes 10–16 mm long, 2–3 mm wide, 41–47 segments; longest specimen 23 mm long, 3 mm wide, 63 segments. Paratype of *Poly-*

Fig. 8. *Gorgoniapolynoe galapagensis,* A–E, holotype (USNM 80085); F, G, paratype (USNM 80086): A, Right cirrigerous parapodium from segment 3, posterior view; B, Right cirrigerous parapodium from segment 10, posterior view; C, Right elytrigerous parapodium from segment 11, anterior view, acicula dotted; D, Notoseta from same; E, Lower, middle and upper neurosetae from same, with detail of tips; F, Right middle cirrigerous parapodium, posterior view, style of dorsal cirrus missing; G, Right middle elytrigerous parapodium, anterior view, acicula dotted. Scales = 0.2 mm for A–C, F, G; 0.1 mm for D, E.

noe uschakovi, removed from pink coral, 10 mm long, 3 mm wide, 39 segments, plus small posterior regenerating region; other paratype (no. 12) 13 mm long, 3 mm wide, 43 segments.

Body elongate, linear, flattened dorsoventrally, tapering posteriorly. First pair of elytra large, covering prostomium, modified: oval chitinous area on lateral half, with scattered oval microtubercles and bottle-shaped micropapillae, and enclosed in wide, medial and narrow, lateral non-chitinous areas (Fig. 9A, C). Following elytra smaller, oval, attached eccentrically, denser around place of attachment (Fig. 9A, D–F). Dorsal cirri with cylindrical cirrophores on poste-

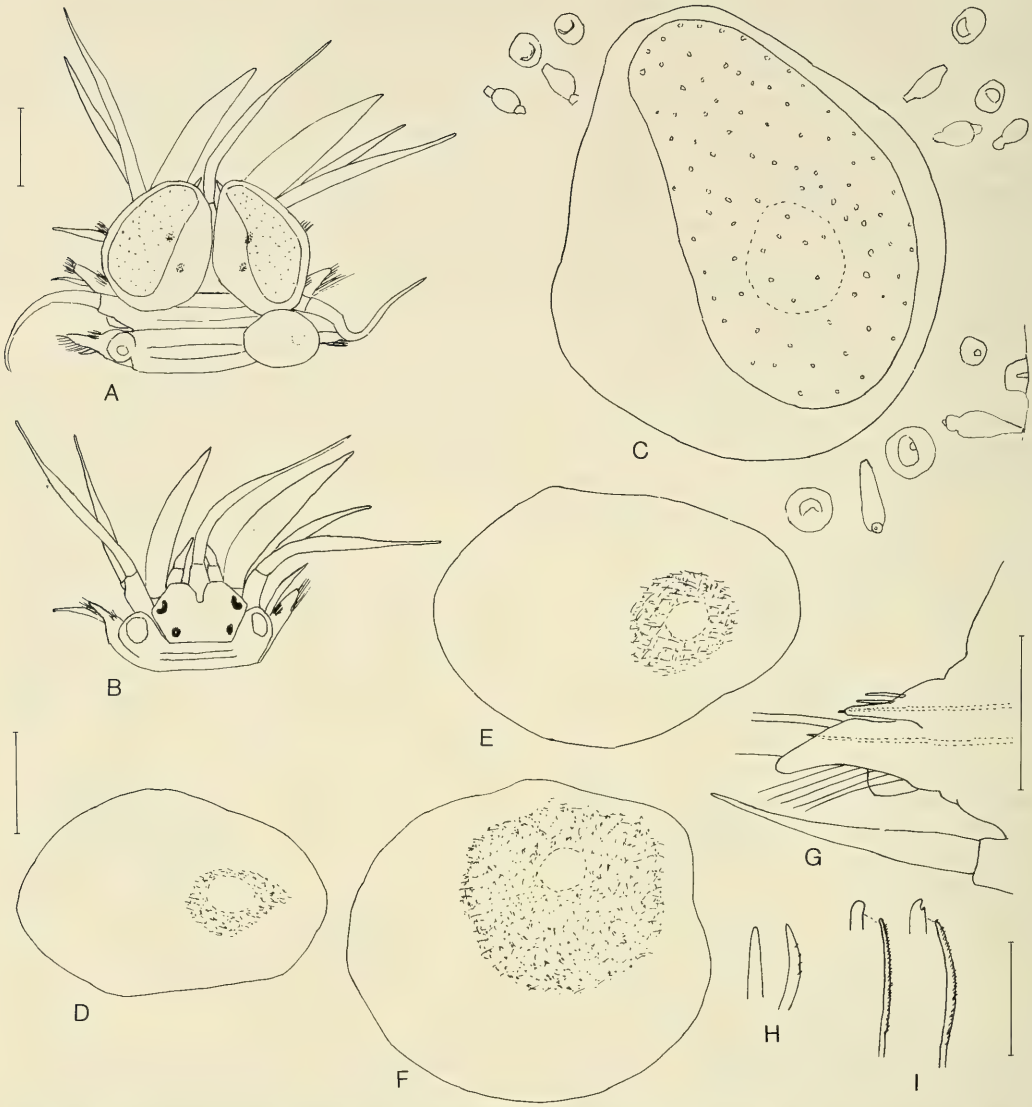


Fig. 9. *Gorgoniapolynoe guadalupensis,* holotype (USNM 80088): A, Dorsal view of anterior end, left 2nd elytron missing; B, Dorsal view of anterior end, elytra removed; C, Right 1st elytron from segment 2, with detail of microtubercles and micropapillae; D, Right 2nd elytron from segment 4; E, Right 3rd elytron from segment 5; F, Right middle elytron; G, Right elytrigerous parapodium from segment 2, anterior view, acicula dotted; H, Notosetae from same; I, Lower and upper neurosetae from same, with detail of tips. Scales = 0.5 mm for A, B; 0.2 mm for C–F; 0.2 mm for G; 0.1 mm for H, I.

rior sides of notopodia and long styles extending far beyond neurosetae, with scattered, clavate micropapillae, and filamentous tips; dorsal tubercles nodular (Figs. 10A, 11B).

Bilobed prostomium with anterior lobes truncate, without cephalic peaks; ceratophore of median antenna in anterior notch, with long, tapering style; ceratophores of lateral antennae inserted lateroventrally, removed from median antenna; styles short, subulate; palps stout, tapered, slightly short-

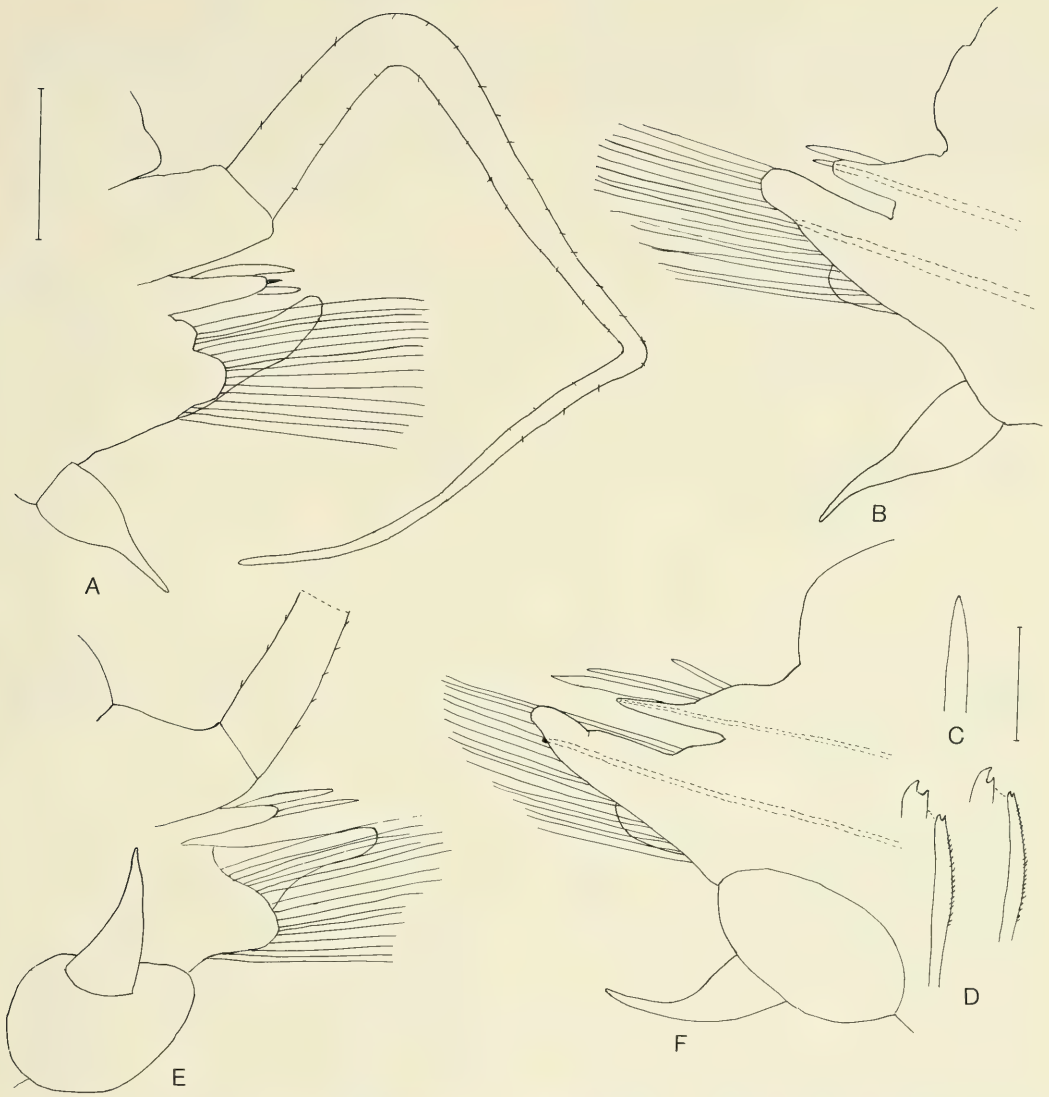


Fig. 10. *Gorgoniapolynoe guadalupensis,* holotype (USNM 80088): A, Right cirrigerous parapodium from segment 8, posterior view; B, Right elytrigerous parapodium from segment 9, anterior view, acicula dotted; C, Notoseta from same; D, Middle and upper neurosetae from same, with detail of tips; E, Right middle cirrigerous parapodium, posterior view, long style of dorsal cirrus incompletely shown; F, Right middle elytrigerous parapodium, anterior view, acicula dotted. Scales = 0.2 mm for A, B, E, F; 0.1 mm for C, D.

er than median antenna; 2 pairs of moderately sized eyes, anterior pair in region of greatest width of prostomium, larger than posterolateral pair (Figs. 9B, 11A). Tentaculophores lateral to prostomium, achaetous; dorsal and ventral tentacular cirri similar to median antenna, dorsal ones slightly longer than ventral ones (Figs. 9B, 11A). Segment 2 with first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri (Fig. 9B, G); notosetae few (2), extending to tip of notopodium; 1 smooth, acicular, 1 curved with 4 spinose rows (Fig. 9H); neurosetae with

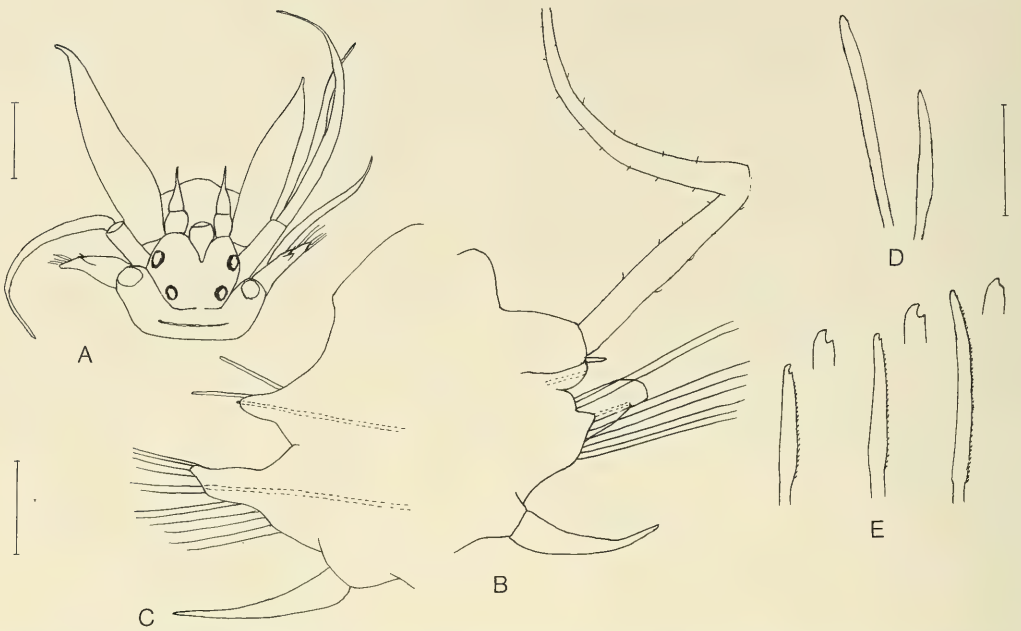


Fig. 11. *Gorgoniapolynoe guadalupensis,* paratype of *Polynoe uschakovi* (USNM 134352): A, Dorsal view of anterior end, styles of median antenna, left dorsal tentacular and buccal cirri missing; B, Right cirrigerous parapodium from segment 10, posterior view, 3 of 4 notosetae hidden from view, tip of dorsal cirrus broken; C, Right elytrigerous parapodium from segment 19, anterior view, acicula dotted; D, Notosetae; E, Lower, middle and upper neurosetae, with detail of tips. Scales = 0.5 mm for A; 0.2 mm for B, C; 0.1 mm for D, E.

spinose rows, upper and middle ones with notched tips, few lower ones with bulbous tips (Fig. 9I). Extended pharynx with 9 dorsal and 9 ventral border papillae and 2 pairs of light amber-colored jaws.

Biramous parapodia with notopodium subconical, shorter and smaller than neuropodium; neuropodium with prominent presetal conical acicular lobe and stout projecting supraacicular process; postsetal lobe shorter, rounded (Figs. 10A, B, E, F, 11B, C). Notosetae few (1–3), extending to about tips of neuropodia, smooth, acicular (Figs. 10C, 11D); some notosetae with few spinous rows (Britayev 1981, fig. 1:3b). Neurosetae with faint spinose rows, upper ones with slightly longer spinose regions, all with bifid or notched tips (Figs. 10D, 11E). Ventral cirri short, thick basally, subulate (Fig. 10A, B); beginning about segment 11, with thickened area below ventral cirri (Fig. 10E, F). Nephridial papillae small, beginning on segment 6. Pygidium with pair of long anal cirri.

Etymology.—The species is named for the collecting area, Guadalupe Island.

Biology.—*Gorgoniapolynoe guadalupensis* was found in tunnels formed by coenenchymal expansions of *Corallium imperiale* Bayer (Gorgonacea: Corallidae), Britayev 1981, fig. 1:9, removed by F. M. Bayer, M. H. Pettibone, and L. Mullineaux.

Distribution.—Eastern Central Pacific Ocean, off Baja California, Guyot Ridge, in 600–2000 meters.

Gorgoniapolynoe caeciliae (Fauvel, 1913), new combination
Figs. 12–14

Polynoe caeciliae Fauvel, 1913:24, fig. 7A–D; 1914:69, pl. 4:figs. 1–6, 18–19; 1923: 82, fig. 31a–h.—Belloc, 1953:4.—Hartmann-Schröder, 1985:31, figs. 1–11 (part, not Indian Ocean).

Material examined.—Eastern North Atlantic Ocean: Gulf of Gascony, 45°05′N, 9°54′W, 1241 m, Prince de Monaco sta 2743, 27 Jul 1908, on *Corallium johnsoni,* 2 syntypes of *Polynoe caeciliae* (MOM; parapodia only, USNM 80098). Off Portugal, 40°33′N, 9°26′W, 1170 m, *Thalassa* sta Y405, 1 Sep 1972, on *Corallium niobe,* ident. by M. Grasshoff, from G. Hartmann-Schröder, 1 specimen (USNM 133356).

Western North Atlantic Ocean: Caribbean Sea, West Indies, off St. Vincent, Lesser Antilles, 13°34′N, 61°03′W, 512 m, *Albatross* sta 2753, 4 Dec 1886, on *Candidella imbricata,* 2 specimens, removed by F. M. Bayer (USNM 21123); 8 specimens, removed by M. Pettibone (USNM 80091). Straits of Florida, east of St. Lucie Inlet, 27°06′N, 79°32′W, 677–659 m, R/V *Gerda* cruise 6333, sta G170, 29 Jun 1963, on holotype of *Corallium niobe,* 3 specimens, removed by F. M. Bayer (USNM 133357). Off Georgia, 30°44′N, 79°26′W, 805 m, *Albatross* sta 2415, 1 Apr 1885, on *Acanthogorgia aspera,* 2 specimens, removed by F. M. Bayer (USNM 80090).

Description.—Syntype of *P. caeciliae* 15 mm long, 2 mm wide, 47 segments. Figured specimen from off Portugal 16 mm long, 3.2 mm wide, 51 segments. Body elongated, almost cylindrical, wider in anterior half, tapering posteriorly. First pair of elytra (not described by Fauvel or Hartmann-Schröder) large, covering prostomium, modified: crescent-shaped area on lateral side transparent, chitinous, with scattered rounded microtubercles and oval micropapillae (Figs. 12A, B, 14A, B); following elytra smaller, oval, leaving middorsum uncovered, smooth or with some scattered micropapillae, denser on large area around place of attachment to elytrophore (Figs. 12C, D, 14A, C; Fauvel 1914, pl. 4:figs. 6, 18). Dorsal cirri with cylindrical cirrophores on posterior sides of notopodia, with styles long, extending far beyond tips of parapodia (Figs. 12A, 13A, E, 14A, F, I). Dorsal tubercles inflated.

Bilobed prostomium much wider than long, with lobes rounded anteriorly, without cephalic peaks; ceratophore of median antenna in anterior notch, with long, tapering style; ceratophores of lateral antennae inserted lateroventrally, removed from median antenna; styles short, subulate; palps stout, about as long as median antenna; 2 pairs of large eyes (Figs. 12A, 14A; Fauvel 1914, pl. 4:fig. 5). Tentaculophores lateral to prostomium, achaetous; dorsal and ventral tentacular cirri long, similar to median antenna, dorsal longer than ventral (Figs. 12A, 14A). Segment 2 with first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri (Figs. 12A, 14A). Extended pharynx with 9 dorsal and 9 ventral border papillae and 2 pairs of jaws (Fig. 14A).

Biramous parapodia with notopodium in form of subconical acicular lobe; neuropodium longer and wider than notopodium, with diagonally truncate presetal acicular lobe, projecting dorsally and shorter, rounded postsetal lobe projecting ventrally, thus appearing bilobed (Figs. 12E, F, 13A, B, D, E, 14E, F, I; Fauvel 1914, pl. 4:fig. 19; Hartmann-Schröder 1985, figs. 1, 2). Notosetae few (2–3, rarely missing), stout, acicular (Figs. 12E–G, 14E–G, I; Fauvel 1914, pl. 4: figs. 4, 19); Hartmann-Schröder 1985, figs. 1–3). Neurosetae about as stout as notosetae, with fine spinose rows and slightly hooked tips, mostly with small or rudimentary secondary tooth (Figs. 12H, 13C, 14H; Fauvel 1914, pl. 4:figs. 1–3; Hartmann-Schröder 1985, figs. 4, 5). Ventral cirri stout, subulate, nearly as long as or longer than tips of neuropodia (Figs. 12E, F, 13A, B, D, E; Fauvel 1914, pl. 4:fig. 19); enlarged bulbous areas medial to ventral cirri, beginning about segment 10, with ventral cirri directed posteriorly (Figs. 13D, 14D, F, I). Nephridial papillae small, cylindrical, beginning on segment 6. Pygidium with pair of long anal cirri.

Biology.—Fauvel (1913:24) reported the syntypes of *G. caeciliae* from the Gulf of

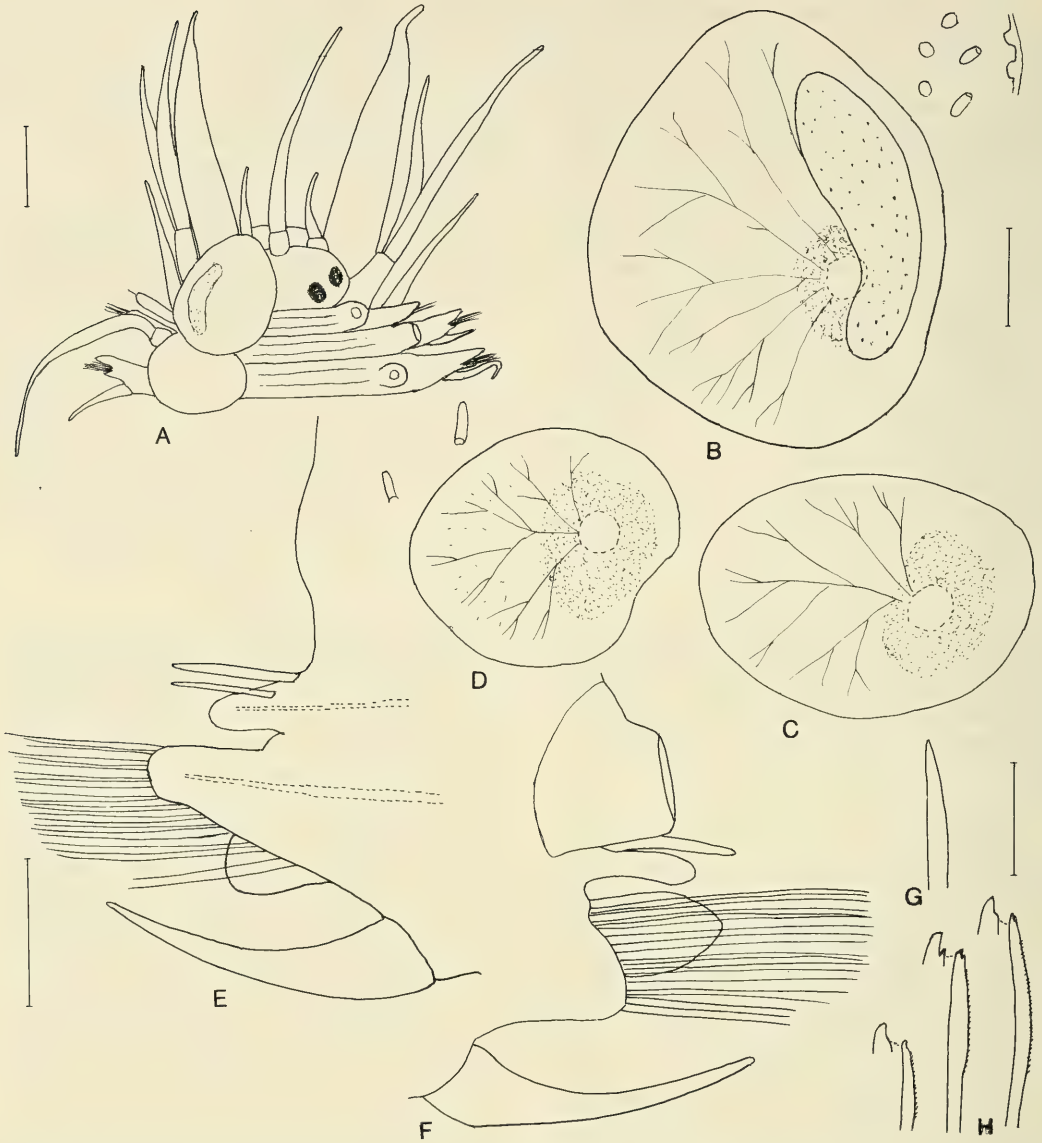


Fig. 12. *Gorgoniapolynoe caeciliae,* A–D, specimen from off Portugal (USNM 133356); E–H, parapodia of syntype of *Polynoe caeciliae* (from MOM, USNM 80098): A, Dorsal view of anterior end, right elytra of segments 2 and 4 and style of dorsal cirrus of segment 3 not shown, left parapodia of segment 2 not developed, right parapodia small, crowded; B, Right 1st elytron from segment 2, with detail of microtubercles and micropapillae; C, Right 2nd elytron from segment 4; D, Right 7th elytron from segment 13, with detail of micropapillae; E, Right elytrigerous parapodium from anterior region, anterior view, acicula dotted; F, Right cirrigerous parapodium from anterior region, posterior view, style of dorsal cirrus broken off; G, Notoseta from same; H, Lower, middle and upper neurosetae from same, with detail of tips. Scales = 0.5 mm for A; 0.2 mm for B–D; 0.2 mm for E, F; 0.1 mm for G, H.

Gascony on *Corallium johnsoni* Gray (as *Pleurocorallium johnstonii*) (Gorgonacea: Coralliidae). Hartmann-Schröder (1985:33) identified numerous specimens of the species from the Gulf of Gascony, off Portugal, Cape Verde Islands, Canary Islands, and Madeira, with *Corallium niobe* Bayer and *C. tricolor* (Johnson); the polynoids were

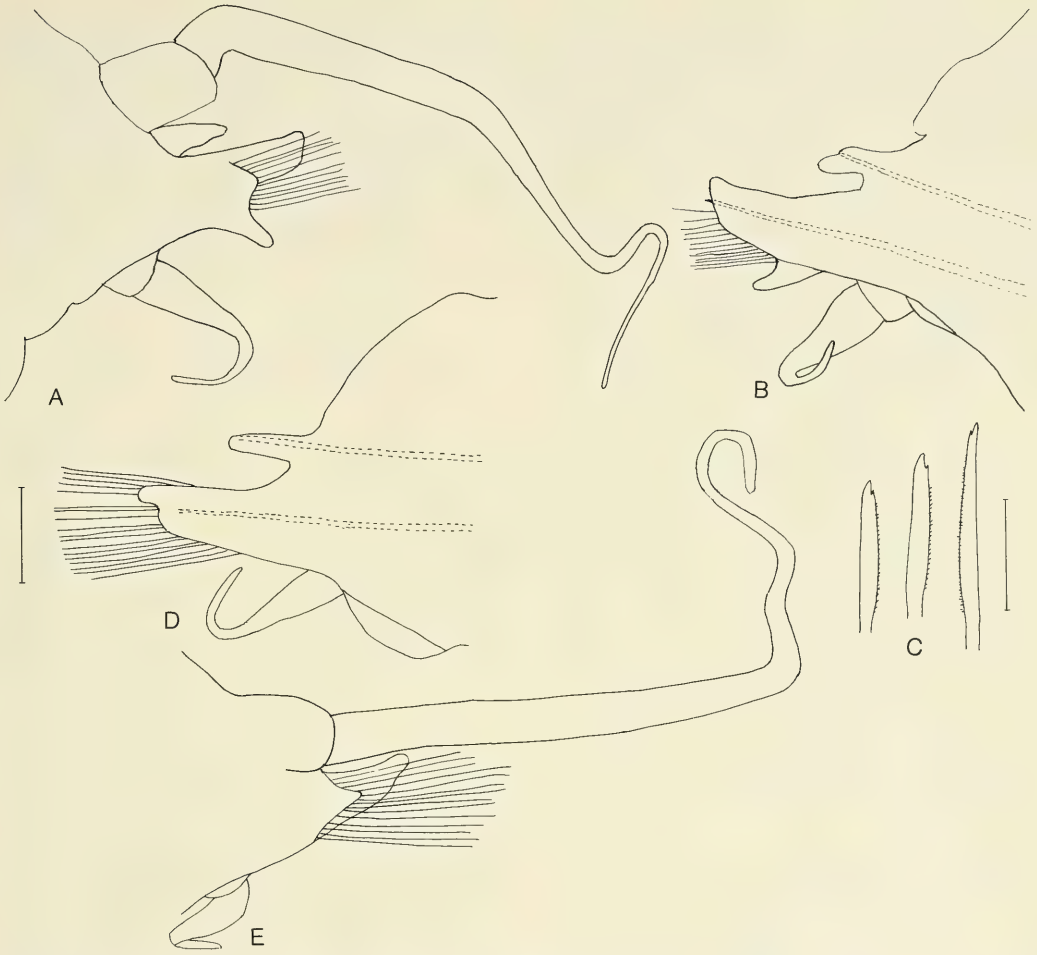


Fig. 13. *Gorgoniapolynoe caeciliae,* specimen from off Portugal (USNM 133356): A, Right cirrigerous parapodium from segment 12, posterior view; B, Right elytrigerous parapodium from segment 13, anterior view, acicula dotted; C, Lower, middle and upper neurosetae from same; D, Right elytrigerous parapodium from segment 29, anterior view, acicula dotted; E, Right cirrigerous parapodium from segment 30, posterior view. Scales = 0.2 mm for A, B, D, E; 0.1 mm for C.

removed by H. Zibrowius and the corals were identified by M. Grasshoff.

From the Straits of Florida, specimens were found on the holotype fragments of *Corallium niobe* Bayer. They were reported by F. M. Bayer (1964:476, figs. 5, 7) as follows: "The polychaete worms live among the polyps on the front of the branches, where they induce abnormal growth of the branchlets which produce covered tunnels through which the worms travel. The covered galleries begin as small branchlets arching upward from the sides of the branches, which meet and ultimately fuse, forming almost solid tunnels with only a few small openings along the sides (Fig. 7). The terminal parts of the branches inhabited by worms are flattened on the front surface and have raised margins (Fig. 5)." The specimens are identified herein as *G. caeciliae.*

From the Lesser Antilles, *G. caeciliae* was found on *Candidella imbricata* (Johnson) (Gorgonacea: Primnoidae), in tunnels formed by enlarged basal scales of the polyps. From off Georgia, the polynoids were found with *Acanthogorgia aspera* Pourtalès

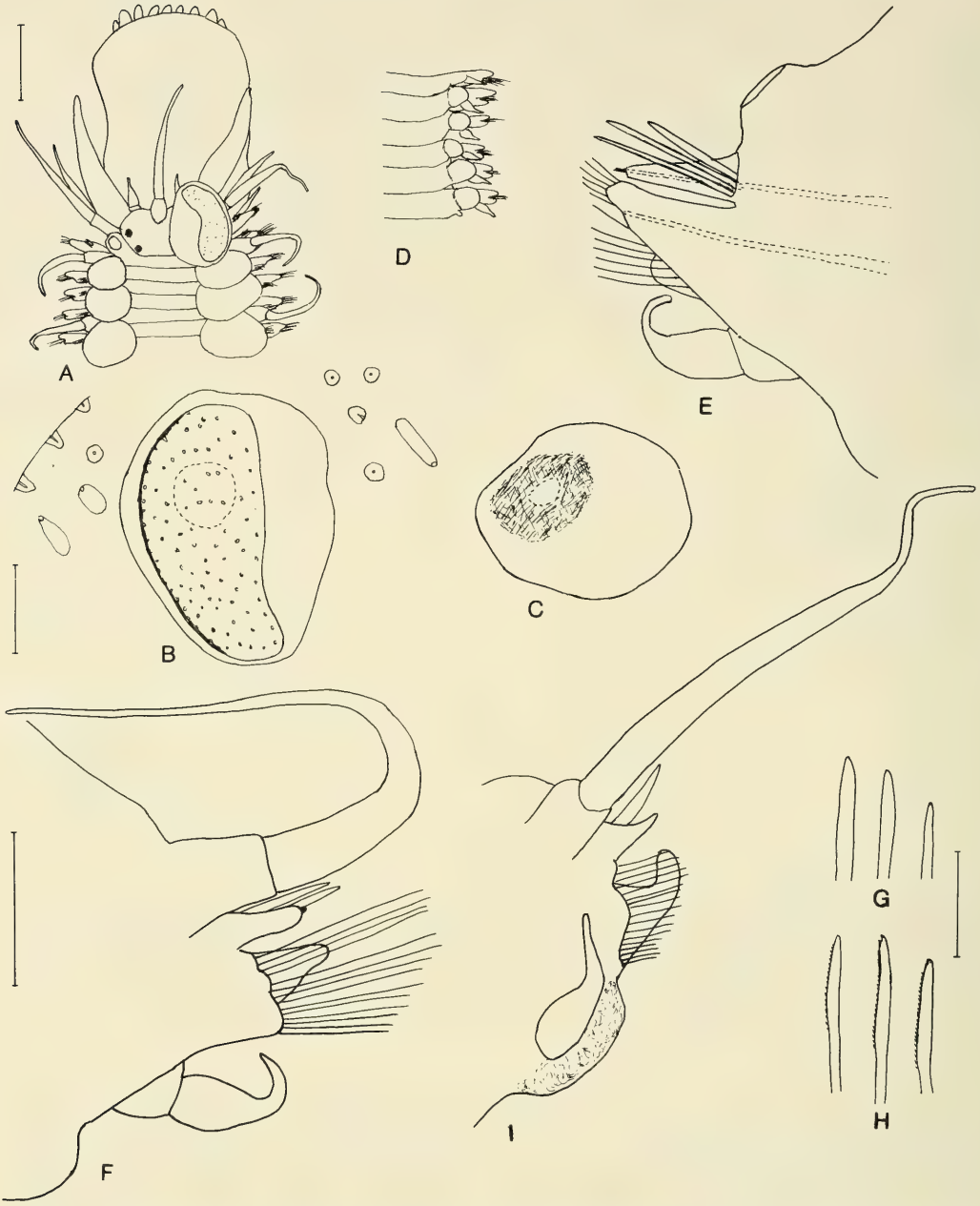


Fig. 14. *Gorgoniapolynoe caeciliae,* specimen from Lesser Antilles (USNM 21123): A, Dorsal view of anterior end, pharynx fully extended, left 1st elytron removed; B, Left 1st elytron from segment 2, with detail of microtubercles and micropapillae; C, Left middle elytron; D, Ventral view of left side of segments 9–14, showing bulbous areas near bases of ventral cirri; E, Right elytrigerous parapodium from anterior region, anterior view, acicula dotted; F, Right cirrigerous parapodium from anterior region, posterior view; G, Notosetae from same; H, Upper, middle and lower neurosetae from same; I, Right cirrigerous parapodium from posterior region, posterior view. Scales = 0.5 mm for A, D; 0.2 mm for B, C; 0.2 mm for E, F, I; 0.1 mm for G, H.

(Gorgonacea: Acanthogorgiidae), in tunnels formed by expanded bases of the polyps and expansions of the coenenchyme.

Distribution.—Eastern North Atlantic Ocean, from Gulf of Gasgony, off Portugal, Cape Verde, Canary, and Madeira islands; Western North Atlantic Ocean, from Caribbean Sea, Straits of Florida, and off Georgia, in 512–1543 meters.

Gorgoniapolynoe corralophila
(Day, 1960), new combination
Fig. 15

Harmothoe corralophila Day, 1960:278, fig. 2a–e; 1967:72, fig. 1.11.a–f.—Stock, 1986: 71, 72.

Material examined.—South Atlantic Ocean: off south coast of Cape Province, South Africa, 34°51′N, 23°41′E, 183 m, South Coast Dredging sta 207, 20 Nov 1960, on *Allopora bithalamus,* J. H. Day, collector, 2 specimens (BMNH 1961.19.5/6; elytra and parapodia, USNM 53531).

Description.—Length 15 mm, with 37 segments. Body broad, tapering posteriorly. Elytra 15 pairs, covering dorsum. First 3 pairs of elytra modified: large chitinous area with conical microtubercles and micropapillae; first pair circular, with narrow, bare margin (Day 1960, fig. 2a; 1967, fig. 1.11.b); 2nd pair elongate oval, with narrow, bare margin (Fig. 15A, B); 3rd pair with wider, bare margin. Following elytra large, elongate oval, smooth, except for few papillae, denser around place of attachment to elytrophore (Fig. 15C; Day 1960, fig. 2b; 1967, fig. 1.11.c). Dorsal cirri with large cylindrical cirrophores on posterior sides of notopodia, bulbous basally, with long styles extending beyond tips of neurosetae; dorsal tubercles bulbous (Fig. 15A, E; Day 1960, fig. 2c; 1967, fig. 1.11.d).

Bilobed prostomium wider than long, anterior lobes wide, subtriangular, with small peaks; median antenna with large ceratophore in anterior notch, style long, with filamentous tip; lateral antennae with ceratophores inserted lateroventrally, removed from median antenna, styles short, subulate; palps stout, tapered, about as long as median antenna; 2 pairs of eyes rather large, anterior pair in region of greatest width of prostomium, much larger than posterior pair (Fig. 15A; Day 1967, fig. 1.11.a). Tentaculophores lateral to prostomium, achaetous (2 setae shown by Day); dorsal and ventral tentacular cirri similar to median antenna (Fig. 15A; Day 1967, fig. 1.11.a). Segment 2 with first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri (Fig. 15A; Day 1967, fig. 1.11.a). Pharynx not extended.

Biramous parapodia with notopodia subconical, almost as long as neuropodia; neuropodia with long conical presetal acicular lobe, with small digitiform supraacicular process, and shorter, rounded postsetal lobe (Fig. 15D, E; Day 1960, fig. 2c; 1967, fig. 1.11.d). Notosetae numerous, forming spreading bundle, short and longer, with widely-spaced spinose rows and rather long, bare, tapered, blunt tips (Fig. 15D–F; Day 1960, fig. 2d; 1967, fig. 1.11.e). Neurosetae very numerous, with spinose rows and bifid, hooked tips, upper ones more slender, with longer spinose regions (Fig. 15D, E, G; Day 1960, fig. 2e; 1967, fig. 1.11.f). Ventral cirri short, subulate (Fig. 15D, E; Day 1960, fig. 2c). Nephridial papillae short, bulbous, beginning on segment 11.

Biology.—*Gorgoniapolynoe corralophila* was reported by Day (1960) in the South Atlantic Ocean off South Africa, in 183 m, on *Allopora bithalamus* Brock (Stylasterina: Stylasteridae), in galls in the shape of open tunnels on the sides of the coral. The species was reported by Stock (1986:71.72, identified by G. Hartmann-Schröder), associated with the stylasterid corals *Stylaster* sp. and *Conopora* sp., near Réunion Island in the Indian Ocean, in 350–750 m, and with *Cryptohelia* sp. (Stylasteridae) near New Caledonia, SW Pacific Ocean, in 585–600 m.

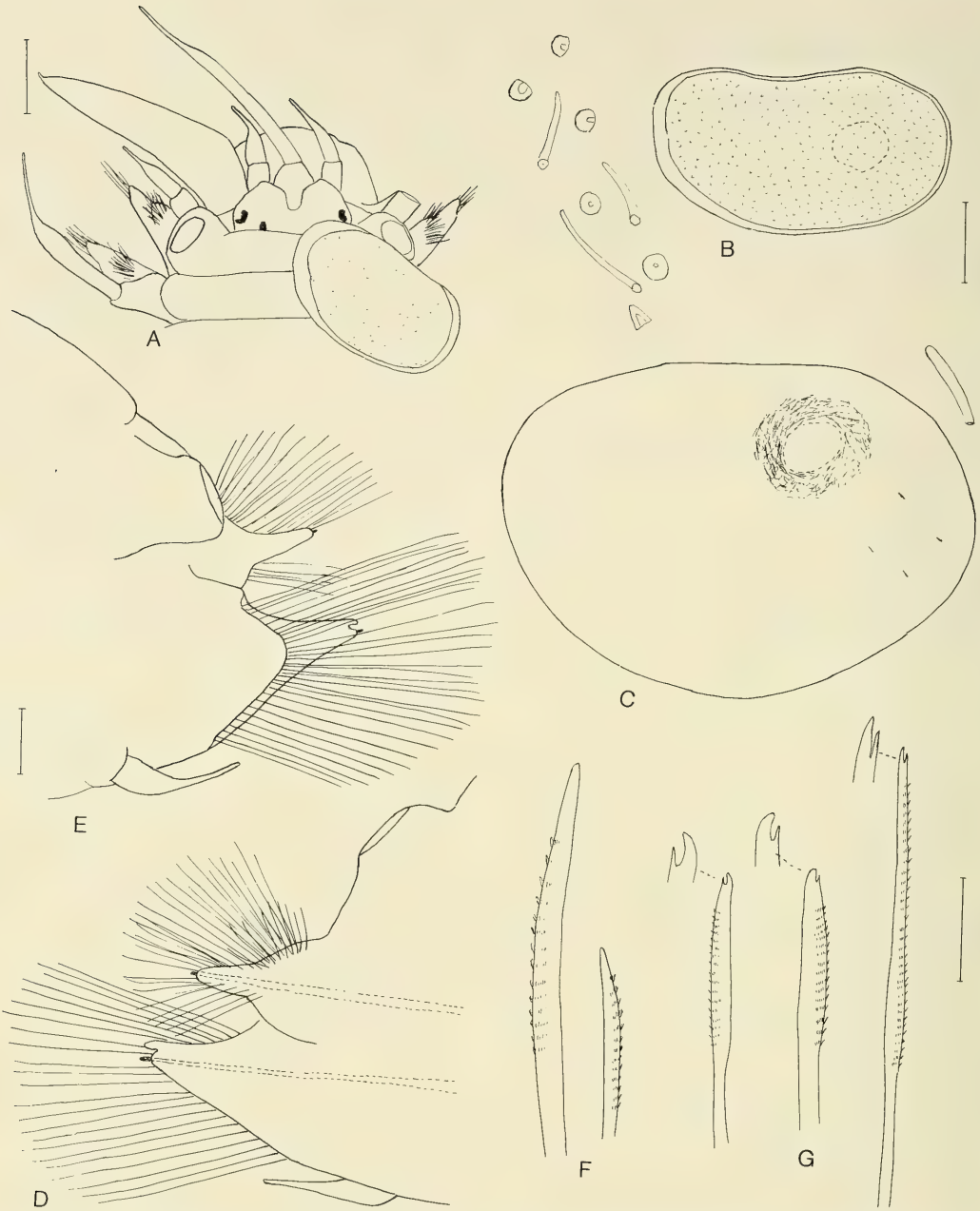


Fig. 15. *Gorgoniapolynoe corralophila,* specimens from South Africa (BMNH 1961.19.5/6; USNM 53531): A, Dorsal view of anterior end, pharynx partially extended, right palp, 1st pair of elytra and right dorsal and ventral and left ventral tentacular cirri missing, left dorsal tentacular cirrus small, regenerating, 2nd right elytron from segment 4 shown; B, Right 2nd elytron from segment 4, with detail of microtubercles and papillae; C, Right middle elytron, with detail of papilla; D, Right middle elytrigerous parapodium, anterior view, acicula dotted; E, Right middle cirrigerous parapodium, posterior view, style of dorsal cirrus missing; F, Long and short notosetae; G, Lower, middle and upper neurosetae, with detail of tips. Scales = 0.5 mm for A; 0.5 mm for B, C; 0.2 mm for D, E; 0.1 mm for F, G.

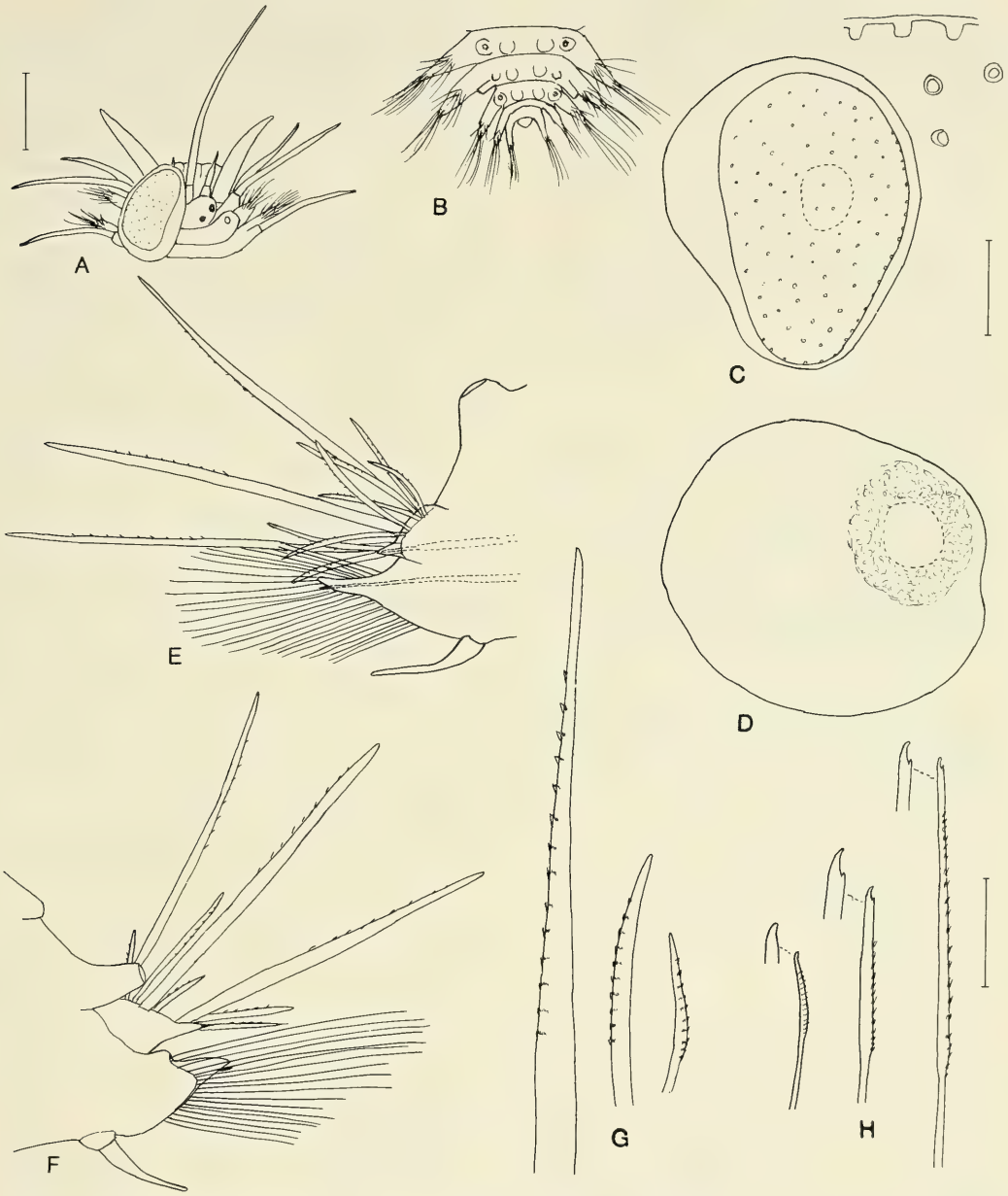


Fig. 16. *Gorgoniapolynoe pelagica,* holotype (USNM 80092): A, Dorsal view of anterior end, including segments 1–3; B, Dorsal view of posterior end, including segments 21–25; C, Right 1st elytron from segment 2, with detail of microtubercles; D, Right 5th elytron from segment 9; E, Right elytrigerous parapodium from segment 9, anterior view, acicula dotted; F, Right cirrigerous parapodium from segment 10, posterior view, style of dorsal cirrus missing; G, Long and shorter notosetae; H, Lower, middle and upper neurosetae, with detail of tips. Scales = 0.5 mm for A, B; 0.2 mm for C–F; 0.1 mm for G, H.

Distribution.—South Atlantic Ocean, South Africa; Indian Ocean, Réunion Island; Southwest Pacific Ocean, New Caledonia, in 72–750 meters.

Gorgoniapolynoe pelagica, new species
Fig. 16

Material examined.—Western North Atlantic Ocean: off Bermuda, 31°39′N, 63°52′W, 0–1750 m, USNM Ocean Acre Program, R/V *Sands* cr 6, sta 6-6N, 26 Apr 1969, Gibbs and Roper, collectors, holotype (USNM 80092).

Description.—Holotype 5 mm long, 3 mm wide including setae, 25 segments. Body elongate, oval, flattened ventrally, arched dorsally. Elytra 12 pairs, on segments 2, 4, 5, 7, continuing on alternate segments to 23. First pair of elytra modified: central part amber-colored, chitinous, translucent, with scattered oval microtubercles, enclosed in bare margin, widest on medial side (Fig. 16A, C). Following elytra large, oval, delicate, denser around place of attachment to elytrophore (Fig. 16D). Dorsal cirri with cylindrical cirrophores on posterior sides of notopodia; styles long, tapered, extending beyond setae; dorsal tubercles nodular (Fig. 16A, B, F). Additional paired rounded tubercles on dorsal side of posterior segments 21–23, medial to elytrophores and dorsal tubercles (Fig. 16B).

Bilobed prostomium with lobes rounded anteriorly, without cephalic peaks; median antenna with ceratophore in anterior notch, style long, slender, with filamentous tip; lateral antennae with ceratophores inserted lateroventrally, removed from median antenna, styles short, with filamentous tips; palps stout, tapered; 2 pairs of moderately sized eyes, anterior pair larger than posterior pair (Fig. 16A). Tentaculophores lateral to prostomium, achaetous; dorsal and ventral tentacular cirri similar to but shorter than median antenna (Fig. 16A). Segment 2 with first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri (Fig. 16A). Pharynx not extended.

Biramous parapodia with notopodium rounded, with projecting acicular process on lower side, almost as long as neuropodium; larger neuropodium with subconical presetal acicular lobe with supraacicular process; postsetal lobe shorter, rounded (Fig. 16E, F). Notosetae moderate in number, forming radiating bundle, stouter than neurosetae, of 2 kinds: few (3–4) long, straight, extending beyond neurosetae, with spinose rows on distal half and long, bare, pointed tips; and ca. 8 short, curved, with shorter spinose regions and shorter, bare tips (Fig. 16G). Neurosetae numerous, upper ones with long spinose regions and slightly curved tips, with small secondary tooth; middle ones with short spinose regions and bifid tips; lower ones with faint spinose rows and entire, slightly hooked tips (Fig. 16H). Ventral cirri short, subulate, with slender tips (Fig. 16E, F). Pygidium small, conical (Fig. 16B).

Etymology.—The species is named for its presence in the plankton.

Remarks.—The species is referred to *Gorgoniapolynoe* based mainly on the modified first pair of elytra. It differs from its commensal congeners in that it is well adapted for swimming, rather than crawling, with well-developed parapodia, long notosetae and neurosetae. It has only 12 pairs of elytra, instead of 15; and 25 segments, instead of about 40 or more. There is a possibility that *G. pelagica* is a pelagic juvenile stage.

Distribution.—Western North Atlantic Ocean, off Bermuda, in 0–1750 meters.

Acknowledgments

My thanks go to the coral specialists who removed the commensal polynoids from the corals and gave them to me for study, along with the identifications of the corals and additional information. This includes Frederick M. Bayer, Katherine M. Muzik, and

Stephen D. Cairns. Gesa Hartmann-Schröder sent specimens from her studies and Temir A. Britayev sent two paratypes. The manuscript benefitted from the reviews by Brigitte Hilbig, Frederick M. Bayer, and an anonymous reviewer.

Literature Cited

Bayer, F. M. 1964. The genus *Corallium* (Gorgonacea: Scleraxonia) in the western North Atlantic Ocean.—Bulletin of Marine Science of the Gulf and Caribbean 14:465–478.

Belloc, G. 1953. Catalogue des types de Polychètes du Musée Océanographique de Monaco.—Bulletin de Institut Océanographique 1027:1–12.

Britayev, T. A. 1981. Two new species of commensal polynoids (Polychaeta, Polynoidae) and bibliography on polychaetes, symbionts of Coelenterata.—Zoologischesky Zhurnal 60(6):817–823. (In Russian)

Cairns, S. D. 1983. Antarctic and subantarctic Stylasterina (Coelenterata: Hydrozoa).—Biology of the Antarctic Seas XIII, Antarctic Research Series 38(2):61–164.

Day, J. H. 1960. The Polychaet fauna of South Africa. Part 5. Errant species dredged off cape coasts.—Annals of the South African Museum 45:261–373.

———. 1967. A Monograph on the Polychaeta of Southern Africa. Part I. Errantia.—Publication British Museum (Natural History), London, No. 656:1–458.

Fauvel, P. 1913. Quatrième note préliminaire sur les Polychètes provenant des campagnes de l' "*Hirondelle*" et de la *Princesse-Alice,* ou déposées dans le Musée Océanographique de Monaco.—Bulletin de l'Institut Océanographique, Monaco 270:1–80.

———. 1914. Anélides polychètes non pélagiques provenant des campagnes de l'*Hirondelle* et de la *Princesse-Alice* (1885–1910).—Résultats des Campagnes Scientifiques Monaco 46:1–432.

———. 1923. Polychètes Errantes.—Faune de France 5:1–488.

Hartmann-Schröder, G. 1985. *Polynoe caeciliae* Fauvel (Polynoidae), ein mit Korallen assoziierter Polychaet.—Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 82: 31–35.

Kinberg, J. G. H. 1856. Nya slägten och arter af Annelider.—Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar, Stockholm 12:381–388.

Stock, J. H. 1986. Cases of hyperassociation in the Copepoda (Herphyllobiidae and Nereicolidae).—Systematic Parasitology 8:71–81.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 714–726

POLYNOID POLYCHAETES COMMENSAL WITH ANTIPATHARIAN CORALS

Marian H. Pettibone

Abstract.—Three new genera and new species of commensal Polynoidae: Harmothoinae, having close associations with antipatharian corals, are described: *Antipathipolyeunoa nuttingi* and *Bayerpolynoe floridensis,* from the North Atlantic Ocean off Barbados, Venezuela, and the Gulf Stream off Florida, and *Tottonpolynoe symantipathicola,* from the South Pacific Ocean off New Zealand. Included also in the Key to the Species of Polynoidae associated with antipatharians is the previously described Lepidastheninae, *Benhamipolynoe antipathicola* (Benham, 1927), from off New Zealand.

Many polynoids are found to have close associations with other invertebrates, especially corals, echinoderms, molluscs, and other polychaetes. The group considered herein includes four species of polynoids, three of them represented by new genera and species, collected on five species of antipatharian corals and one gorgonian. This commensal relationship has been noted by some antipatharian coral specialists.

In connection with his study on the fauna of the Gulf Stream at great depths off Florida, de Pourtalès (1867) described a number of antipatharians. Based on collections of the Barbados-Antigua Expedition, Nutting (1919:113) commented on the antipatharians, noting that *Antipathes columnaris* Duchassaing was one of the commonest species collected off Barbados. It resembled a small bottle-brush with stiff-wavy branches thickly implanted on the sides of the straight central stem. Many specimens had hollow tunnels formed by anastomosed twigs, lying along the main stems, induced by the presence of a commensal annelid.

Silberfeld (1911:20–21, pl. 1: figs. 2, 4) described and photographed a new antipatharian from Sagami Bay, Japan, *Parantipathes tenuispina,* with a so-called worm-run on the main stem. In his report on the Antipatharia from the *Terra Nova* voyage off New Zealand, Totton (1923:106–108, figs. 9–11, pl. 2: fig. 5) identified and described two bottle-brush shaped colonies as *P. tenuispina,* both containing worm-runs, where the branchlets of the main branches united as arches, forming the framework of a worm-run.

As indicated by Benham (1927:64, 67), the worm on *P. tenuispina* was removed from the worm-tunnel by Professor J. Arthur Thomson. He described the latticed tunnel as being about 10 cm long, fitted the worm loosely and was formed by an interlacing, and fusion of numerous serrated branchlets that formed an intricate meshwork along the main axis of the coral. The worm was initially submitted to Professor McIntosh and later to W. B. Benham, while working up the polychaetes of the *Terra Nova* Expedition off New Zealand. Benham (1927:64–67, pl. 1: figs. 11–13) described the worm as a new polynoid species, *Lepidasthenia antipathicola.* Later, Pettibone (1970: 201–205, figs. 1–4) reexamined the holotype and referred the species to a new genus, *Benhamipolynoe,* and added to the species records a specimen from the *Siboga* Expedition in the Malay Archipelago, found in an empty tube of an eunicid polychaete, and a specimen from the North Atlantic in the Gulf Stream off Florida, from a *Fish Hawk*

station, associated with the antipatharian *Antipathes columnaris* Duchassaing. *B. antipathicola* is included in the key to the known species of Polynoidae associated with antipatharian corals.

Key to the Known Species of Polynoidae associated with Antipatharian Corals

1. Prostomium lepidasthenoid, lateral antennae inserted terminally on anterior extensions of prostomium, without distinct ceratophores (Pettibone 1970, figs. 1a, 2a, 3a). Parapodia subbiramous, notopodia short conical acicular lobe, without notosetae; neuropodia deeply cut dorsally and ventrally, with subequal, rounded presetal and postsetal lobes, without projecting acicular lobe (Pettibone 1970, fig. 1b, c). Commensal with *Parantipathes tenuispina* Silberfeld and *Antipathes columnaris* Duchassaing .....
.... Lepidastheniinae Pettibone, 1989: *Benhamipolynoe antipathicola* (Benham, 1927)
– Prostomium harmothoid, with cephalic peaks; ceratophores of lateral antennae distinct, inserted ventrally (Figs. 1A, 3A, 5A). Parapodia biramous, notopodia with notosetae; neuropodia with subconical presetal acicular lobe and short, rounded postsetal lobe (Figs. 1F, G, 4A, B, 5B, C) Harmothoinae Willey, 1902 2
2. Notopodia nearly as long as neuropodia; neuropodia without presetal subacicular process (Fig. 5B, C). Elytra 16 pairs, on segments 2, 4, 5, 7, alternate segments to 26, 29, 32, 36, with dorsal cirri on posterior segments. Commensal with *Parantipathes* sp. and gorgonian *Sclerisis macquarina* Bayer & Stefani .....
... *Tottonpolynoe symantipatharia,* n. gen., n. sp.
– Notopodia much shorter than neuropodia; neuropodia with presetal subacicular process (Figs. 1F, G, 4A, B) 3
3. Elytra 15 pairs, confined to anterior region, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, with dorsal cirri on posterior segments. Commensal with *Antipathes columnaris* Duchassaing .....
.. *Bayerpolynoe floridensis,* n. gen., n. sp.
– Elytra numerous pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 33, 35, continuing on alternate segments. Commensal with *Antipathes tanacetum* Pourtalès ..
..... *Antipathipolyeunoa nuttingi,* n. gen., n. sp.

Family Polynoidae Kinberg, 1856
Subfamily Harmothoinae Willey, 1902
Antipathipolyeunoa, new genus

Type species.—*Antipathipolyeunoa nuttingi,* new species.

Diagnosis.—Body elongate, flattened, with sides nearly parallel, tapering posteriorly; segments numerous (up to 84). Elytra and bulbous elytrophores numerous pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 33, continuing on alternate segments to near end of body. Elytra moderate in size, circular to oval, leaving middorsum uncovered, without fringes of papillae or tubercles. Dorsal cirri on nonelytrigerous segments, with short cirrophores and long styles; dorsal tubercles inconspicuous. Prostomium bilobed, with subtriangular anterior peaks, 3 antennae and 2 palps; ceratophore of median antenna in anterior notch of prostomium, with long style; lateral antennae with distinct ceratophores inserted ventrally, with short styles; palps relatively short; 2 pairs of large eyes on posterior half of prostomium. Tentaculophores of segment I lateral to prostomium, achaetous, with 2 pairs of long tentac-

ular cirri; prominent bulbous facial tubercle. Buccal segment (II) without nuchal fold, with first pair of elytra, biramous parapodia, and long ventral buccal cirri; pharynx with 9 pairs of border papillae and 2 pairs of jaws. Parapodia biramous; notopodia small, conical, on anterodorsal face of larger neuropodia; notosetae relatively few (9–2), about as stout as neurosetae, acicular, with faint spinose rows; neuropodia with longer subconical presetal acicular lobe, with projecting subacicular process, and shorter rounded postsetal lobe; neurosetae relatively few (6–11), rather stout, with falcate tips and faint spinose rows. Ventral cirri rather long, extending to tips of neuropodia. Nephridial papillae short, beginning on segment 6. Pygidium with pair of long anal cirri. Commensal with antipatharians.

Remarks.—Of the genera of Harmothoinae with elongate bodies, numerous segments, and numerous elytra continuing to near end of the body, *Antipathipolyeunoa* is closest to *Polyeunoa* McIntosh, 1885, as emended by Bergström (1916) and Pettibone (1969:45). The new genus differs mainly by having a prominent subacicular process on the presetal acicular lobe of the neuropodium, lacking in *Polyeunoa.*

Etymology.—*Antipathipolyeunoa* is based on its close relationship with antipatharians and the polynoid genus *Polyeunoa.* Gender feminine.

Antipathipolyeunoa nuttingi,
new species
Figs. 1, 2

Material examined.—North Atlantic Ocean, Carribean Sea: Barbados, off Payne's Bay Church, 91 m, 31 May 1918, Barbados-Antigua Expedition 1918, sta 65, on antipatharian "A," C. C. Nutting, collector, removed by F. M. Bayer, identified as *Antipathes tanacetum* Pourtalès by D. M. Opresko, holotype (USNM 80097). Venezuela, NE of Farallon Centinela, 10°57′N, 65°59′W, 70 m, R/V *Pillsbury* sta P736, on *Antipathes tanacetum* Pourtalès, removed by D. M. Opresko, 3 paratypes (USNM 136587).

Description.—Holotype 21 mm long, 3 mm wide with setae, 82 segments. Complete paratype 25 mm long, 3 mm wide, 84 segments. Body elongate, slender, slightly flattened, with sides nearly parallel, tapering gradually posteriorly. Coloration with nearly continuous middorsal reddish brown longitudinal band, with some spots on bases of dorsal cirri and some midventral pigmentation. Elytra numerous pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 33, 35, continuing on alternate segments to 73, 77, with dorsal cirri on posterior 5 segments (arrangement somewhat variable on posterior region of paratypes). Elytra round, chalky white, opaque, attached eccentrically; moderate in size, leaving middorsum uncovered, larger anteriorly, becoming smaller posteriorly; without papillae or tubercles (Fig. 2G–I).

Dorsal cirri with short, cylindrical cirrophores posterodorsal to notopodia; styles long, extending far beyond setae; dorsal tubercles indistinct (Figs. 1E, G, 2B).

Bilobed prostomium with wide, subtriangular cephalic peaks; eyes rather large, anterior pair on middle of lateral surface, posterior pair posterolateral; ceratophore of median antenna in anterior notch of prostomium, style long, smooth, with long filamentous tip; lateral antennae with ceratophores inserted ventrally, styles short, with filamentous tips; palps stout, tapered, shorter than median antenna; tentaculophores lateral to prostomium, achaetous; dorsal tentacular cirri long, similar to median antenna, longer than ventral tentacular cirri (Fig. 1A); facial tubercle bulbous. Segment 2 without nuchal lobe, with bulbous elytrophores, biramous parapodia, short conical notopodium with moderate number of notosetae (9), similar to following notosetae; larger neuropodium and neurosetae similar to following neurosetae only more slender; ventral buccal cirri much longer than fol-

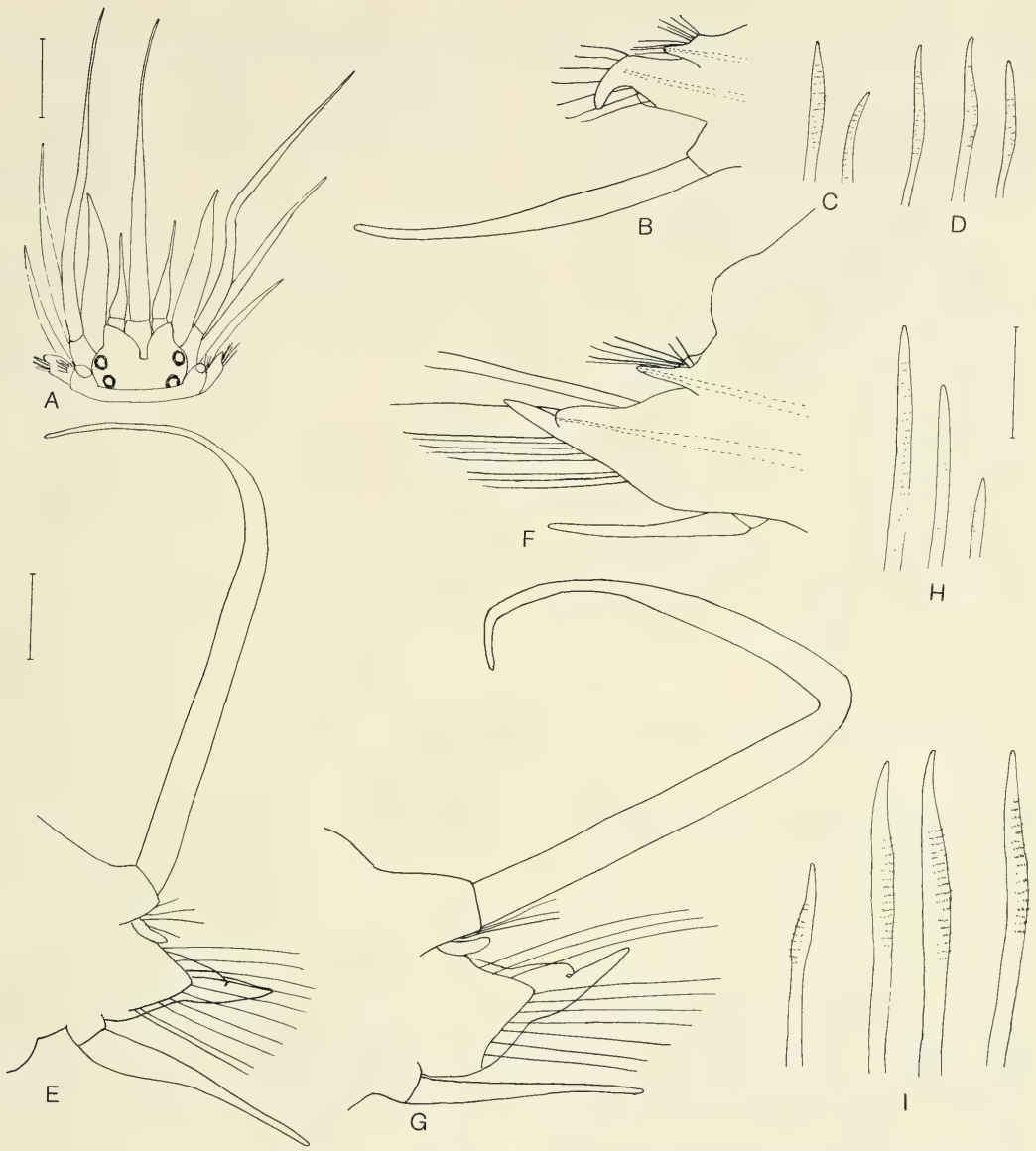


Fig. 1. *Antipathipolyeunoa nuttingi,* holotype: A, Dorsal view of anterior end; B, Right elytrigerous parapodium from segment 2, anterior view, acicula dotted; C, Notosetae from same; D, Lower, middle and upper neurosetae from same; E, Right cirrigerous parapodium from segment 3, posterior view; F, Right elytrigerous parapodium from segment 9, anterior view, acicula dotted; G, Right cirrigerous parapodium from segment 10, posterior view; H, Long and shorter notosetae from same; I, Lower, middle and upper neurosetae from same. Scales = 0.5 mm for A; 0.2 mm for B, E–G; 0.1 mm for C, D, H, I.

lowing ventral cirri, similar to tentacular cirri (Fig. 1A–D). Pharynx (cut open) with 9 pairs of border papillae and 2 pairs of reddish amber-colored jaws.

Biramous parapodia with short conical notopodium with longer acicular lobe on lower side; much large neuropodium with longer subconical presetal acicular lobe with projecting digitiform subacicular process and shorter rounded postsetal lobe (Figs.

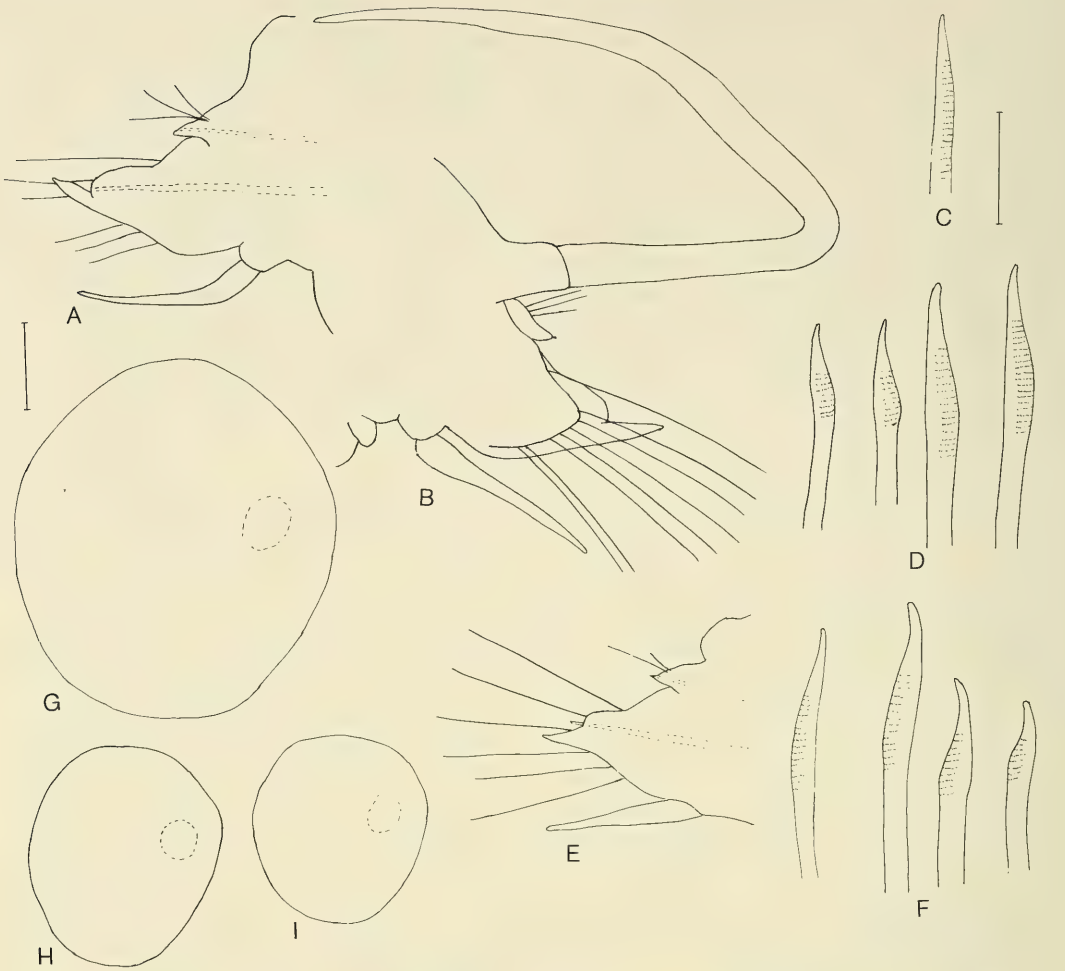


Fig. 2. *Antipathipolyeunoa nuttingi,* holotype: A, Right elytrigerous parapodium from middle region, anterior view, acicula dotted; B, Right cirrigerous parapodium from middle region, posterior view; C, Notoseta from same; D, Lower, middle and upper neurosetae from same; E, Right elytrigerous parapodium from posterior region, anterior view, acicula dotted; F, Upper, middle and lower neurosetae from same; G, Right elytron from segment 9; H, Right elytron from middle region; I, Right elytron from posterior region. Scales = 0.2 mm for A, B, E, G–I; 0.1 mm for C, D, F.

1B, E–G, 2A, B, E). Notosetae almost as stout as neurosetae, short, acicular, with faint spinose rows, relatively few (9 on 2nd notopodium, 7 on 9th, 3 on middle, 2 on posterior) (Figs. 1B, C, F–H, 2A–C, E). Neurosetae rather short, acicular, with falcate tips and faint spinose rows; all similar, varying slightly in size and length of spinose regions; relatively few (7 on 2nd neuropodium, 11 on 9th, 8–6 on middle, 6 on posterior) (Figs. 1B, D, F, I, 2A, B, D–F). Ventral cirri tapering, relatively long, extending about to tips of neuropodia or beyond (Figs. 1E–G, 2A, B, E).

Pygidium small, rounded lobe with dorsal anus and pair of anal cirri. Nephridial papillae small, rounded, beginning on segment 6 (Fig. 2B).

Associations.—Antipathipolyeunoa nuttingi was found living commensally on the

antipatharian *Antipathes tanacetum* Pourtalès. In his study on the antipatharians of the Barbados-Antigua Expedition 1918, C. C. Nutting (1919:113) reported that the commensal annelids were found in hollow tubes lying along the main stems of the antipatharians.

Etymology.—The species is named for Professor Charles Cleveland Nutting, leader of the Barbados-Antigua Expedition of 1918 and specialist on hydroids and the Alcyonaria.

Bayerpolynoe, new genus

Type species.—*Bayerpolynoe floridensis,* new species.

Diagnosis.—Body elongate, flattened, with sides nearly parallel, tapering posteriorly; segments numerous (up to 85). Elytra and bulbous elytrophores 15 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32. Elytra large, elongate-oval, covering dorsum in anterior region, leaving large posterior region uncovered, without fringes of papillae or tubercles. Dorsal cirri on non-elytrigerous segments, with short cirrophores and long styles; dorsal tubercles inconspicuous. Prostomium bilobed, with distinct cephalic peaks, 3 antennae and 2 palps; ceratophore of median antenna in anterior notch of prostomium; lateral antennae with ceratophores inserted ventrally; 2 pairs of large eyes on posterior half of prostomium. Tentaculophores of segment I lateral to prostomium, each with few setae and pair of dorsal and ventral tentacular cirri; prominent bulbous facial tubercle. Buccal segment (II) without nuchal fold, with first pair of elytra, biramous parapodia, and long ventral buccal cirri; pharynx with 9 pairs of border papillae and 2 pairs of jaws. Parapodia biramous; notopodia small, conical, on anterodorsal face of larger neuropodia; notosetae moderate in number, about as stout as neurosetae, acicular, with faint spinose rows; neuropodia with longer subconical presetal acicular lobe, with projecting subacicular process, and shorter rounded postsetal lobe; neurosetae moderate in number, acicular, with faint spinose rows and tapered bare tips. Ventral cirri rather long, extending to tips of neuropodia. Nephridial papillae short, cylindrical, beginning on segment 6. Pygidium damaged. Commensal with antipatharians.

Remarks.—*Bayerpolynoe* agrees with *Antipathipolyeunoa* in having a prominent subacicular process on the presetal acicular lobe of the neuropodia. It differs in having only 15 pairs of elytra confined to the anterior part of the body, instead of numerous pairs, continuing to near the posterior end.

Etymology.—The genus is named for Frederick M. Bayer, in recognition of his studies on the Octocorallia and who has discovered and contributed numerous polynoid commensals to me for study. Gender feminine.

Bayerpolynoe floridensis, new species
Figs. 3, 4

Material examined.—North Atlantic Ocean, Gulf Stream off Key West, Florida, 24°17′N, 81°58′W, 237 m, *Fish Hawk* sta 7280, 14 Feb 1902, on antipatharian *Antipathes columnaris* Duchassaing, removed by F. M. Bayer, identified by D. M. Opresko, holotype (USNM 80079).

Description.—Holotype 27 mm long, 3.5 mm wide with setae, 85 segments. Body elongate, slender, with sides nearly parallel, tapering posteriorly. Coloration with middorsal brownish longitudinal band and pigment spots on cirrophores of dorsal cirri, ventrally with midventral and lateral longitudinal bands. Elytra 15 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, with long region with dorsal cirri only. Elytra rather large, elongate-oval, covering anterior part of body, delicate, without papillae or tubercles; light brownish pigmented rings near border, except on anterior part (Fig. 3F, G). Dorsal cirri with short cylindrical cirrophores and long styles ex-

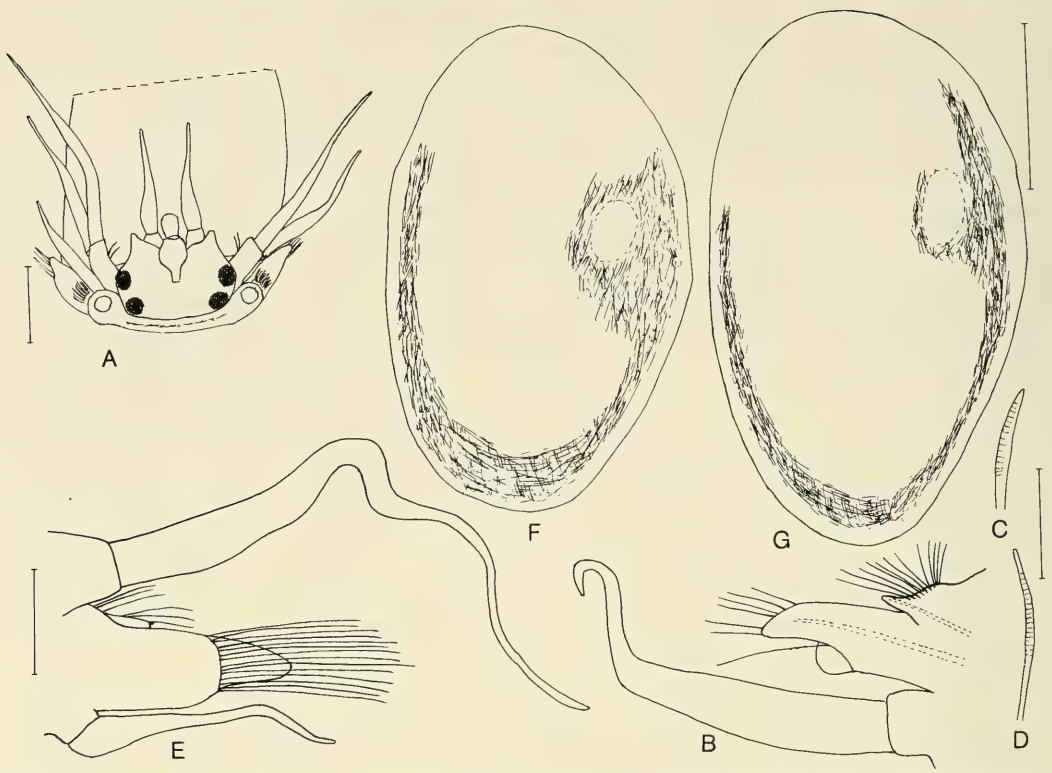


Fig. 3. *Bayerpolynoe floridensis,* holotype: A, Dorsal view of anterior end, pharynx fully extended (only basal part shown), style of median antenna and palps missing; B, Right elytrigerous parapodium of segment 2, anterior view, acicula dotted; C, Notoseta from same; D, Neuroseta from same; E, Right cirrigerous parapodium of segment 3, posterior view; F, Right 6th elytron from segment 11; G, Right 15th elytron from segment 32. Scales = 0.5 mm for A; 0.2 mm for B, E; 0.1 mm for C, D; 0.5 mm for F, G.

tending far beyond setae; dorsal tubercles indistinct (Figs. 3E, 4A, H).

Bilobed prostomium with distinct cephalic peaks; eyes large, anterior pair in region of greatest width, slightly larger than posterolateral pair; ceratophore of median antenna in anterior notch of prostomium, style missing (probably long); lateral antennae with ceratophores inserted ventrally, with short, subulate styles; palps missing; tentaculophores lateral to prostomium, each with 2 setae on inner side and pair of longer dorsal and shorter ventral tentacular cirri; facial tubercle bulbous, between ceratophores of lateral antennae (Fig. 3A). Segment 2 without nuchal lobe, with bulbous elytrophores and biramous parapodia; short conical notopodium with notosetae similar to following; larger neuropodium with neurosetae more slender than following, with rounded tips; ventral buccal cirri much longer than following ventral cirri, similar to tentacular cirri (Fig. 3A–D). Pharynx with 9 pairs of border papillae and 2 pairs of amber-colored jaws.

Biramous parapodia with short conical notopodia with longer acicular lobe on lower side; much larger neuropodia with longer subconical presetal acicular lobe, with projecting digitiform subacicular process, and shorter rounded postsetal lobe (Figs. 3B, E, 4A, B, E, H). Notosetae almost as stout as neurosetae, acicular, short, slightly curved and longer, straight, with faint spinous rows; moderate in number (12 on 2nd notopodium, 14 on 11th, 11 on 32nd, 10 on pos-

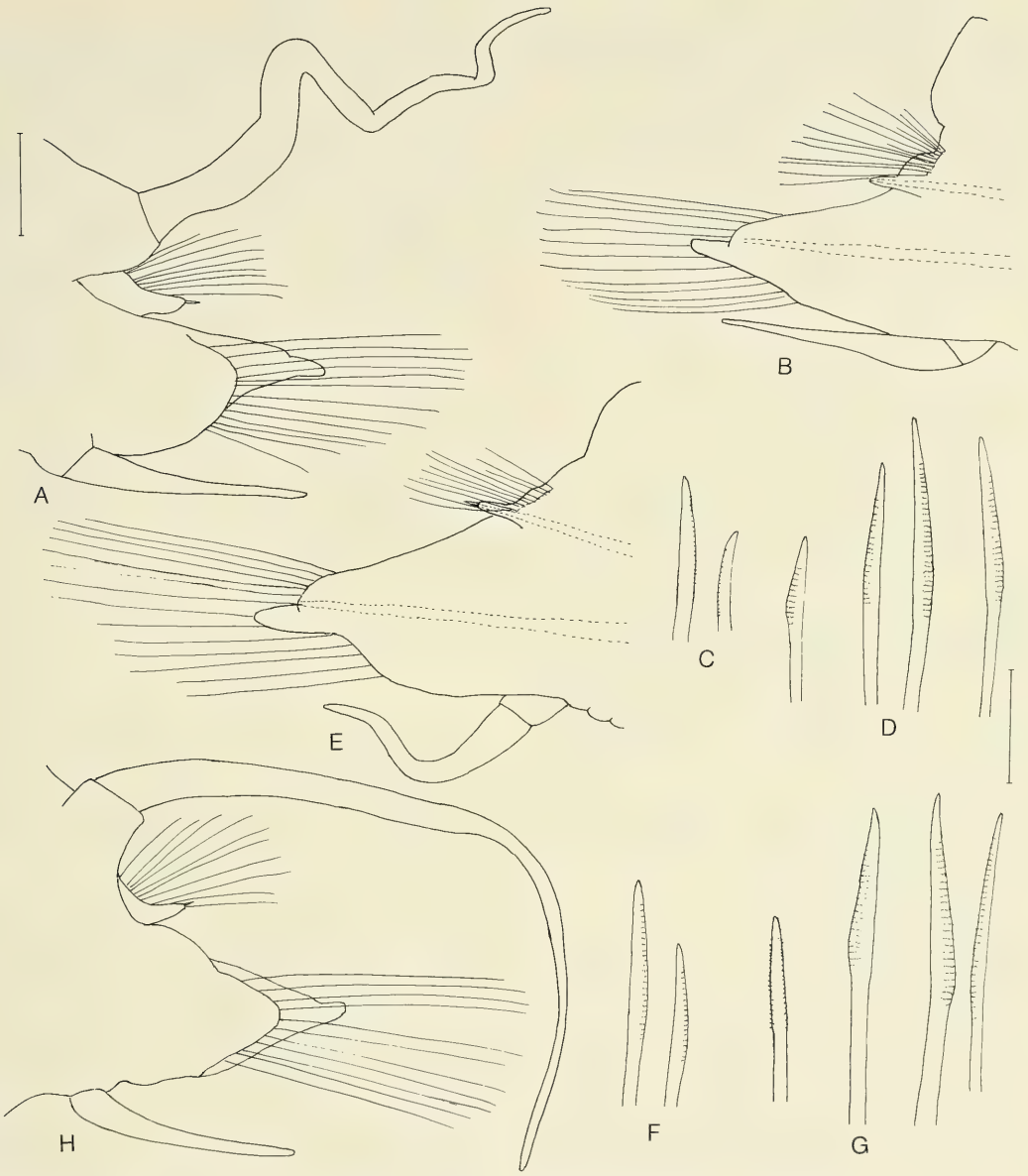


Fig. 4. *Bayerpolynoe floridensis,* holotype: A, Right cirrigerous parapodium from segment 10, posterior view; B, Right elytrigerous parapodium from segment 11, anterior view, acicula dotted; C, Notosetae from same; D, Lower, middle and upper neurosetae from same; E, Right elytrigerous parapodium from segment 32, anterior view, acicula dotted; F, Notosetae from same; G, Lower, middle and upper neurosetae from same; H, Right cirrigerous parapodium from posterior region, posterior view. Scales = 0.2 mm for A, B, E, H; 0.1 mm for C, D, F, G.

terior) (Figs. 3B, C, 4B, C, E, F, H). Neurosetae long, acicular, with tapered blunt tips, all same type, varying slightly in width and length of faint spinose regions; moderate in number (7 on 2nd neuropodium, 13 on 11th, 14 on 32nd, 10 on posterior) (Figs. 3B, D, 4B, D, E, G, H). Ventral cirri tapering, rather long, extending almost to

tips of neuropodia (Figs. 3E, 4A, B, E, H). Pygidium damaged. Nephridial papillae small, beginning on segment 6.

Biology.—*Bayerpolynoe floridensis* was found living commensally on the antipatharian *Antipathes columnaris* Duchassaing.

Etymology.—The species is named for the collecting site off Florida.

Tottonpolynoe, new genus

Type species.—*Tottonpolynoe symantipatharia,* new species.

Diagnosis.—Body elongate, flattened, tapering posteriorly; segments numerous (up to 71). Elytra 16 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 36, with dorsal cirri on following segments. Elytra large, oval, covering dorsum of anterior part of body, without papillae, with or without microtubercles on anterior part. Dorsal cirri on non-elytrigerous segments, with short cirrophores and long styles; dorsal tubercles nodular. Prostomium bilobed, with subtriangular cephalic peaks, 3 antennae and 2 palps; ceratophore of median antenna in anterior notch of prostomium, with long style; lateral antenna with ceratophores inserted ventrally, with short styles; palps relatively short; 2 pairs of large eyes on posterior half of prostomium. Tentaculophores of segment I lateral to prostomium, achaetous, with 2 pairs of long tentacular cirri; without facial tubercle. Buccal segment (II) without nuchal fold, with first pair of elytra, biramous parapodia, and long ventral buccal cirri. Parapodia biramous; notopodia almost as long as neuropodia, with projecting acicular lobe; notosetae moderate in number, acicular, about as stout as neurosetae, appearing smooth; neuropodia with subconical presetal acicular lobe and shorter, rounded postsetal lobe; neurosetae moderate in number, stout, with slightly hooked bare tips and prominent to faint spinose rows. Ventral cirri rather long, extending about to tips of neuropodia. Nephridial papillae short, beginning on segment 6. Commensal with antipatharians and gorgonians.

Etymology.—*Totton,* named for A. Knyvett Totton (1923:97–120, pls. I, II), who reported on commensal polychaetes in connection with his study on the Antipatharia from off New Zealand, plus *polynoe,* from polynoid worm. Gender feminine.

Remarks.—Of the genera in Harmothoinae, with elongate bodies and numerous segments, *Tottonpolynoe* differs by having 16 pairs of elytra, not the usual 15 pairs, confined to the anterior part of the body. The parapodia resemble *Polyeunoa* McIntosh in having the neuropodia with prominent presetal subconical acicular lobes and lacking both supraacicular and subacicular digitiform processes.

Tottonpolynoe symantipatharia,
new species
Figs. 5–7

Material examined.—South Pacific Ocean, off New Zealand, 53°45′W, 159°09′E, 787–842 m, *Eltanin* sta 1416, 9 Feb 1965, in groove on main stem of antipatharian *Parantipathes* sp., removed by S. D. Cairns and identified by D. M. Opresko, holotype (USNM 136585). Off Macquarie Island, south of New Zealand, 56°21′S, 158°28′E, 1684 m, *Eltanin* sta 1423, 12 Feb 1965, in runway on gorgonian *Sclerisis macquariana* Bayer & Stefani, removed by F. M. Bayer, paratype (USNM 136586).

Description.—Holotype 30 mm long, 7 mm wide with setae, 71 segments. Incomplete paratype 21+ mm long, 5 mm wide, 55+ segments. Body elongate, greatly flattened, widest anteriorly, tapering posteriorly. Dorsum brownish banded on segments 12–34. Elytra 16 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 36, with dorsal cirri on posterior segments. Elytra large, oval, covering dorsum in anterior part, leaving posterior segments uncovered, attached eccentrically, delicate, with "veins," without papillae, with few to

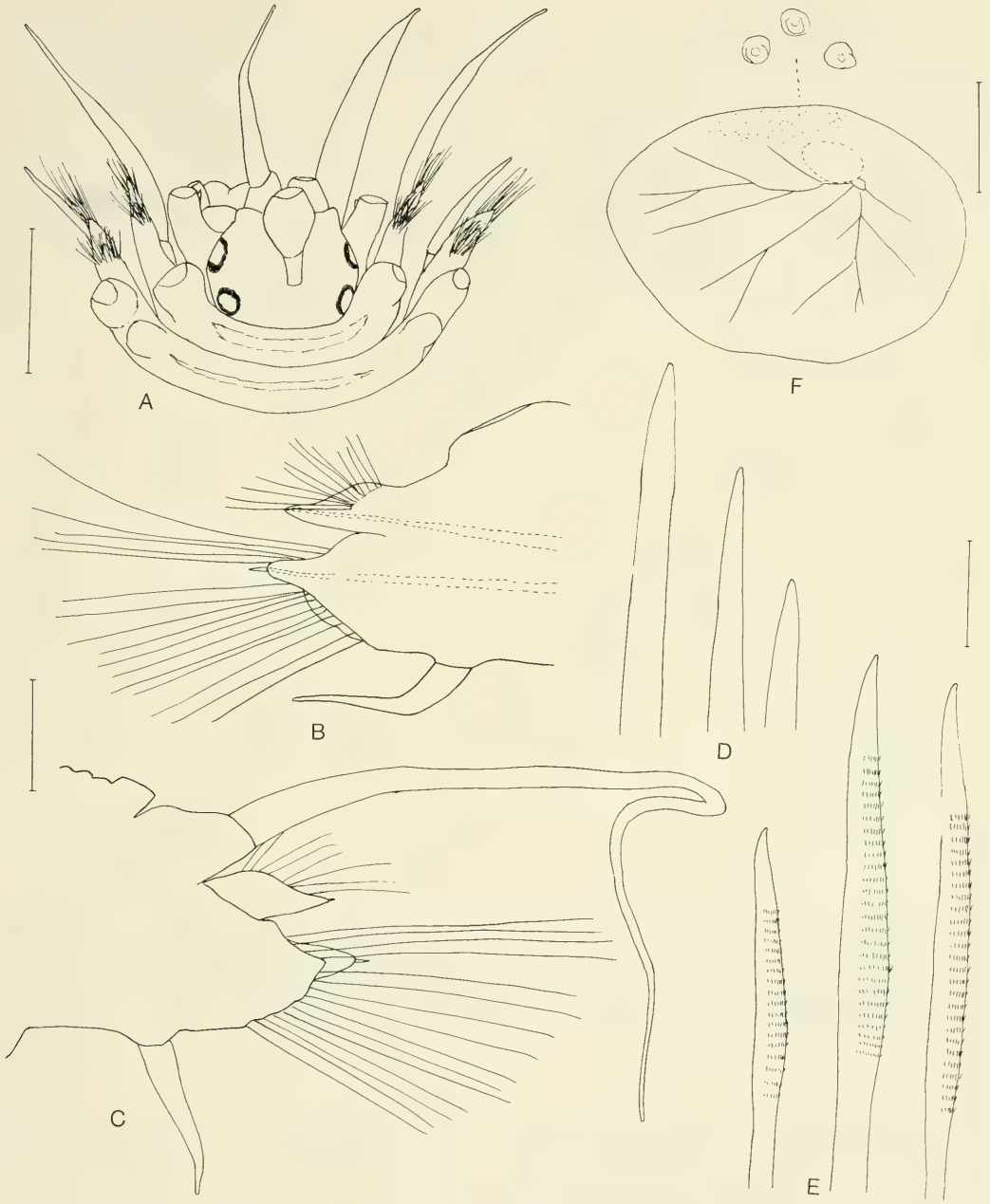


Fig. 5. *Tottonpolynoe symantipatharia,* holotype: A, Dorsal view of anterior end, styles of median antenna, right and left dorsal and ventral tentacular cirri, left palp, and dorsal cirri of segment 3 missing; B, Right elytrigerous parapodium, anterior view, acicula dotted; C, Right cirrigerous parapodium, posterior view; D, Long and shorter notosetae; E, Lower, middle and upper neurosetae; F, Right elytron, with detail of microtubercles. Scales = 1.0 mm for A; 0.5 mm for B, C; 0.1 mm for D, E; 1.0 mm for F.

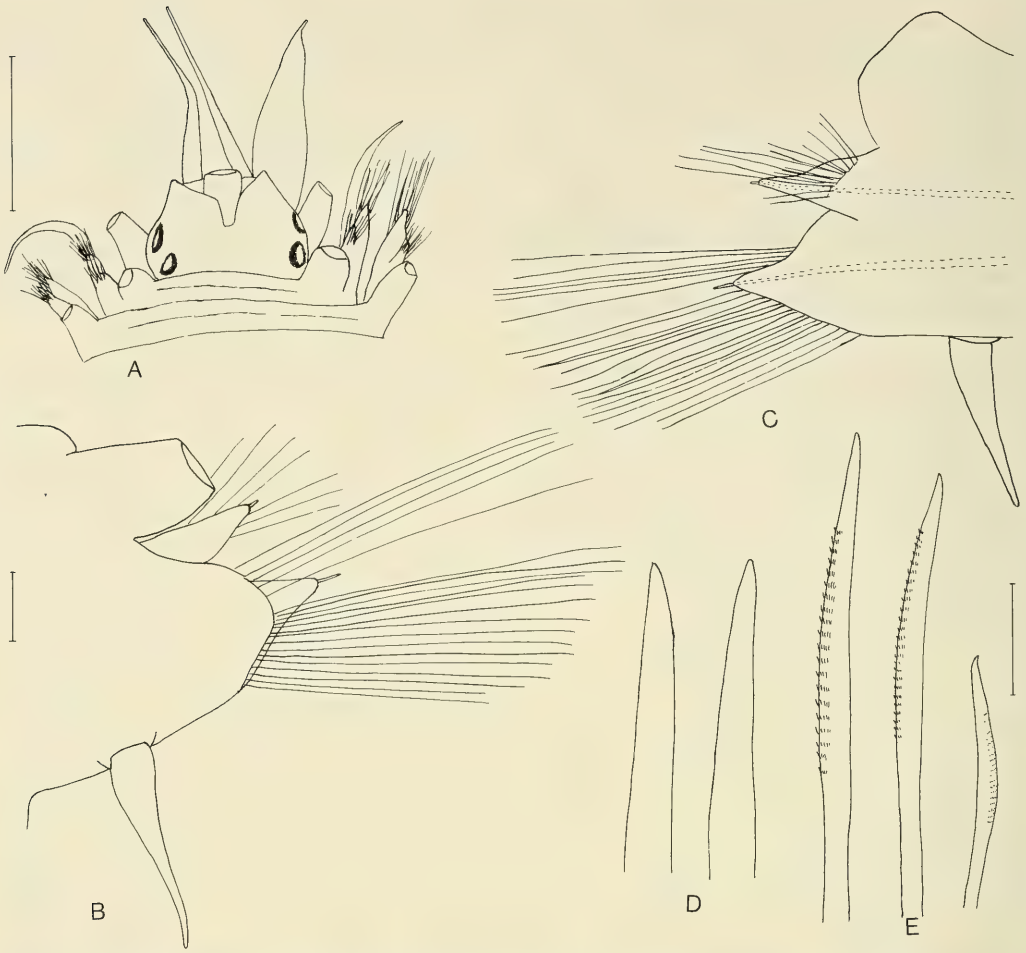


Fig. 6. *Tottonpolynoe symantipatharia,* paratype: A, Dorsal view of anterior end, style of median antenna, right and left tentacular cirri, left palp, and dorsal cirri of segment 3 missing; B, Right cirrigerous parapodium of segment 16, posterior view, dorsal cirrus missing; C, Right elytrigerous parapodium of segment 17, anterior view, acicula dotted; D, Notosetae; E, Upper, middle and lower neurosetae. Scales = 1.0 mm for A; 0.2 mm for B, C; 0.1 mm for D, E.

numerous microtubercles on anterior part of some elytra (Figs. 5F, 7D–F). Dorsal cirri with cylindrical cirrophores dorsal to notopodia, styles very long, tapering to slender tips and extending far beyond setae; dorsal tubercles nodular (Figs. 5A, C, 6A, B, 7A).

Bilobed prostomium with wide, subtriangular anterior peaks; eyes large, anterior pair in region of greatest width of prostomium, slightly larger than posterolateral pair; ceratophore of median antenna in anterior notch of prostomium, style missing (probably long); ceratophores of lateral antennae inserted ventrally, styles rather long, tapered, with filamentous tips; palps stout, tapered; tentaculophores lateral to prostomium, with small acicular lobe on inner side, achaetous; dorsal and ventral tentacular cirri missing (probably long); without facial tubercle (Figs. 5A, 6A). Segment 2 without nuchal lobe, with bulbous elytrophores, biramous parapodia, and long ven-

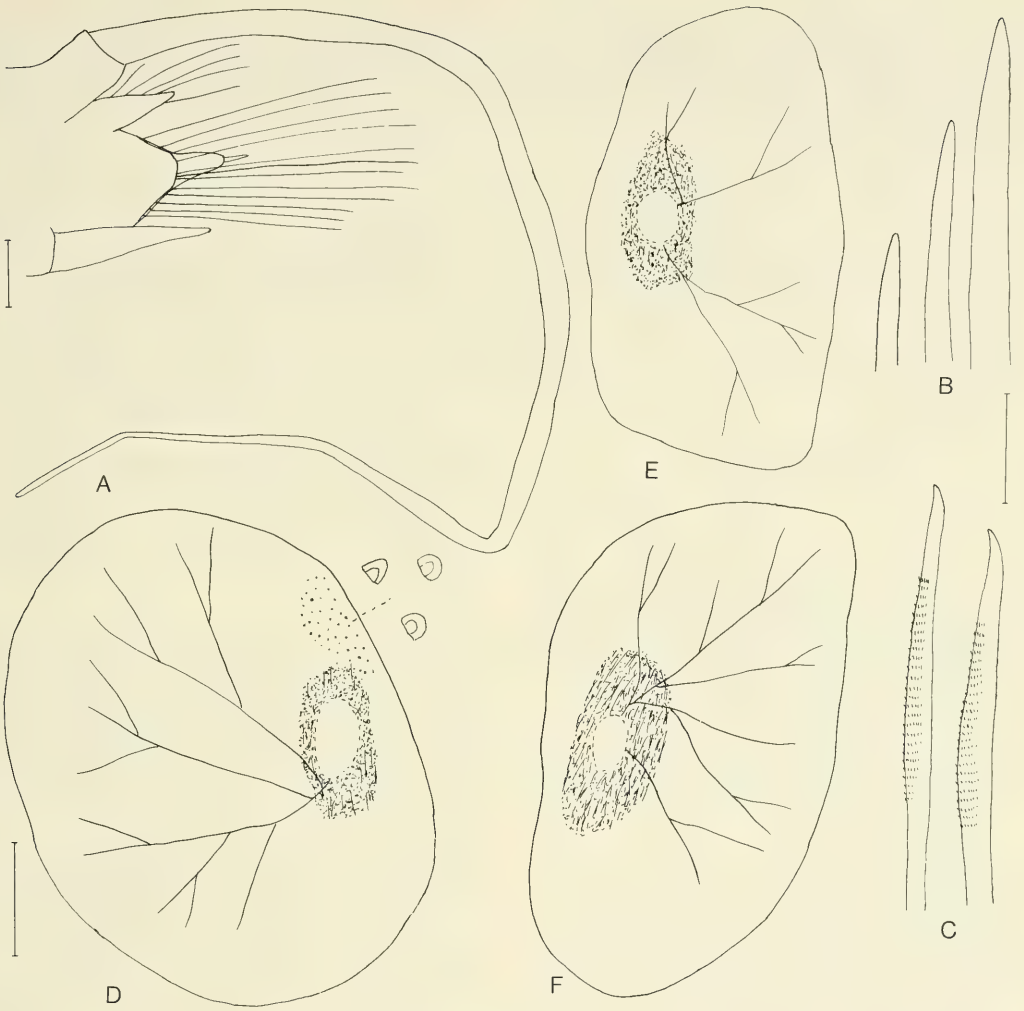


Fig. 7. *Tottonpolynoe symantipatharia*, paratype: A, Right cirrigerous parapodium from segment 40, posterior view; B, Short and longer notosetae; C, Upper and middle neurosetae; D, Right 9th elytron from segment 17, with detail of microtubercles; E, Left 15th elytron from segment 32; F, Left 16th elytron from segment 35. Scales = 0.2 mm for A; 0.1 mm for B, C; 0.5 mm for D–F.

tral buccal cirri (Figs. 5A, 6A). Pharynx not extended.

Biramous parapodia with notopodia almost as long as neuropodia, rounded, with digitiform acicular lobe on lower side; larger neuropodia with longer subconical presetal acicular lobe and shorter rounded to subtriangular postsetal lobe (Figs. 5B, C, 6B, C, 7A). Notosetae moderate in number (about 15), short to long, forming radiating bundle, acicular, about as stout as neurosetae, appearing smooth, with faint close-set striations (Figs. 5B, D, 6C, D, 7A, B). Neurosetae moderate in number (about 16), forming fan-shaped bundle, stout, with slightly hooked bare tips, upper ones slightly more slender, with longer and more prominent spinose rows, middle and lower ones with very faint close-set spinose rows (Figs. 5B, E, 6C, E, 7A, C). Ventral cirri rather

long, tapered, extending almost to tips of neuropodia (Figs. 5B, C, 6B, C, 7A).

Pygidium small, rounded lobe with pair of anal cirri (missing). Nephridial papillae small, beginning on segment 6.

Biology.—*Tottonpolynoe symantipatharia* was found in a groove along the main stem of the antipatharian *Parantipathes* sp. and in a runway on the gorgonian *Sclerisis macquariana* Bayer & Stefani, 1987.

Etymology.—Greek *sym* = with + *antipatharia,* in reference to its association with antipatharians.

Acknowledgments

I wish to thank Frederick M. Bayer, Dennis W. Opresko, and Stephen D. Cairns for the material on which this study is based. The manuscript benefited from the reviews by James A. Blake and Frederick M. Bayer.

Literature Cited

Bayer, F. M., & J. Stefani. 1987. Isididae (Gorgonacea) de Nouvelle-Calédonie nouvelle clé des genres de la famille.—Bulletin du Muséum National d'Histoire Naturelle, Paris ser. 4, 9A(1): 47–106.

Benham, W. B. 1927. Polychaeta.—British Antarctic "Terra Nova" Expedition, 1910.—Natural History Report, Zoology 7(2):47–182.

Bergström, E. 1916. Die Polynoiden des schwedischen Südpolarexpedition 1901–1903.—Zoologiska Bidrag från Uppsala 4:269–304.

Kinberg, J. G. M. 1856. Nya slägten och arter af Annelider.—Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar (Stockholm) 12:381–388.

McIntosh, W. C. 1885. Annelida Polychaeta.—Report on the Scientific Results of the H.M.S. Challenger . . . 1873–76 . . . Zoology 12(34):1–554.

Nutting, C. C. 1919. Barbados-Antigua Expedition, narrative and preliminary report of a zoological expedition from the University of Iowa to the Lesser Antilles under the auspices of the graduate college.—University of Iowa Studies in Natural History 8(3):1–274.

Pettibone, M. H. 1969. The genera *Polyeunoa* McIntosh, *Hololepidella* Willey, and three new genera (Polychaeta, Polynoidae).—Proceedings of the Biological Society of Washington 82:43–62.

———. 1970. Polychaeta errantia of the Siboga Expedition. Part 4: Some additional polychaetes of the Polynoidae, Hesionidae, Nereidae, Goniadidae, Eunicidae, and Onuphidae, selected as new species by the late Dr. Hermann Augener with remarks on other related species.—Siboga-Expeditie 24, 1d:199–270.

———. 1989. A new species of *Benhamipolynoe* (Polychaeta: Polynoidae: Lepidastheniinae) from Australia, associated with the unattached stylasterid coral *Conopora adeta.*—Proceedings of the Biological Society of Washington 102:300–304.

Pourtalès, L. F. de. 1867. Contributions to the fauna of the Gulf Stream at great depths.—Bulletin of the Museum of Comparative Zoology at Harvard College in Cambridge 1(6):103–120.

Silberfeld, E. 1911. Japanische Antipatharien.—Abhandlungen der Mathematisch-Physikalischen Klasse Akademie der Wissenschaften, München 1 Suppl. Bd. 7:1–30.

Totton, A. K. 1923. Coelenterata. Part III. Antipatharia (and their cirripede commensals).—British Antarctic ("Terra Nova") Expedition, 1910 Natural History Report, Zoology 5(3):97–120.

Willey, A. 1902. Polychaeta.—Report on the collections of natural history made in the Antarctic regions during the voyage of the *Southern Cross,* London 12:262–283.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 727–735

LEPEOPHTHEIRUS SPATHA, A NEW SPECIES OF COPEPOD (SIPHONOSTOMATOIDA: CALIGIDAE) PARASITIC ON THE CALIFORNIA HALIBUT FROM SANTA MONICA BAY, CALIFORNIA

Masahiro Dojiri and Robert A. Brantley

Abstract.—*Lepeophtheirus spatha,* new species, is described from the external body surfaces of the California halibut *Paralichthys californicus* (Ayers) collected in Santa Monica Bay, California. The female differs from females of its congeners by the possession of a combination of characters including posterior processes on the genital complex, truncate sternal furcal tines, and a subtriangular leg 5. It appears to be most closely related to *L. paralichthydis* Yamaguti & Yamasu, 1960 which was collected from the body surfaces of *Paralichthys olivaceus* (Temminck & Schlegel) from Japan.

The Environmental Monitoring Division, Bureau of Sanitation, City of Los Angeles, assesses the dilution, movement, and environmental effects of treated effluent discharged into the waters of the Santa Monica Bay, an open coastal embayment bordered by Point Dume to the north and Palos Verdes Point to the south. As part of the monitoring program, the Biology Laboratory conducts quarterly otter trawls which involve the identification, enumeration, length and biomass measurements of demersal fishes and macroinvertebrates at ten designated stations. During the July and November 1989 and February 1990 trawls, several specimens of the parasitic copepod family Caligidae were collected from the body surfaces of the California halibut *Paralichthys californicus* (Ayers). These parasites represent a new species of *Lepeophtheirus* which is described below.

Materials and methods.—The copepods were preserved in 70% ethanol, then cleared in 85% lactic acid for a period of at least 24 hours. They were then measured with an ocular micrometer, and selected specimens were dissected on wooden slides (Humes & Gooding 1964). Illustrations were drawn with the aid of a drawing tube attached to a Nikon Optiphot, HFX-II. Type specimens have been deposited in the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Dissected specimens remain in the collection of the first author.

Systematic Account

Order Siphonostomatoida Thorell, 1859
Family Caligidae Burmeister, 1835
Genus *Lepeophtheirus* Nordmann, 1832
Lepeophtheirus spatha, new species
Figs. 1–5

Material examined.—From external body surface of California halibut *Paralichthys californicus* (Ayres) collected in Santa Monica Bay, California, by the Biology Laboratory, Environmental Monitoring Division, City of Los Angeles: 1 female holotype (USNM 244345) and 20 paratypes (15 females, 3 males, and 1 pair in amplexus; USNM 244346; 1 male dissected on slide) from station A4, 33°34′24″N, 118°31′34″W, in 15 m, on 20 Feb 1990; 3 females (1 dissected) from station C1, 33°59′49″N, 118°42′50″W, in 60 m, on 31 Jul 1989; 2 females and 1 male (dissected on slide) from

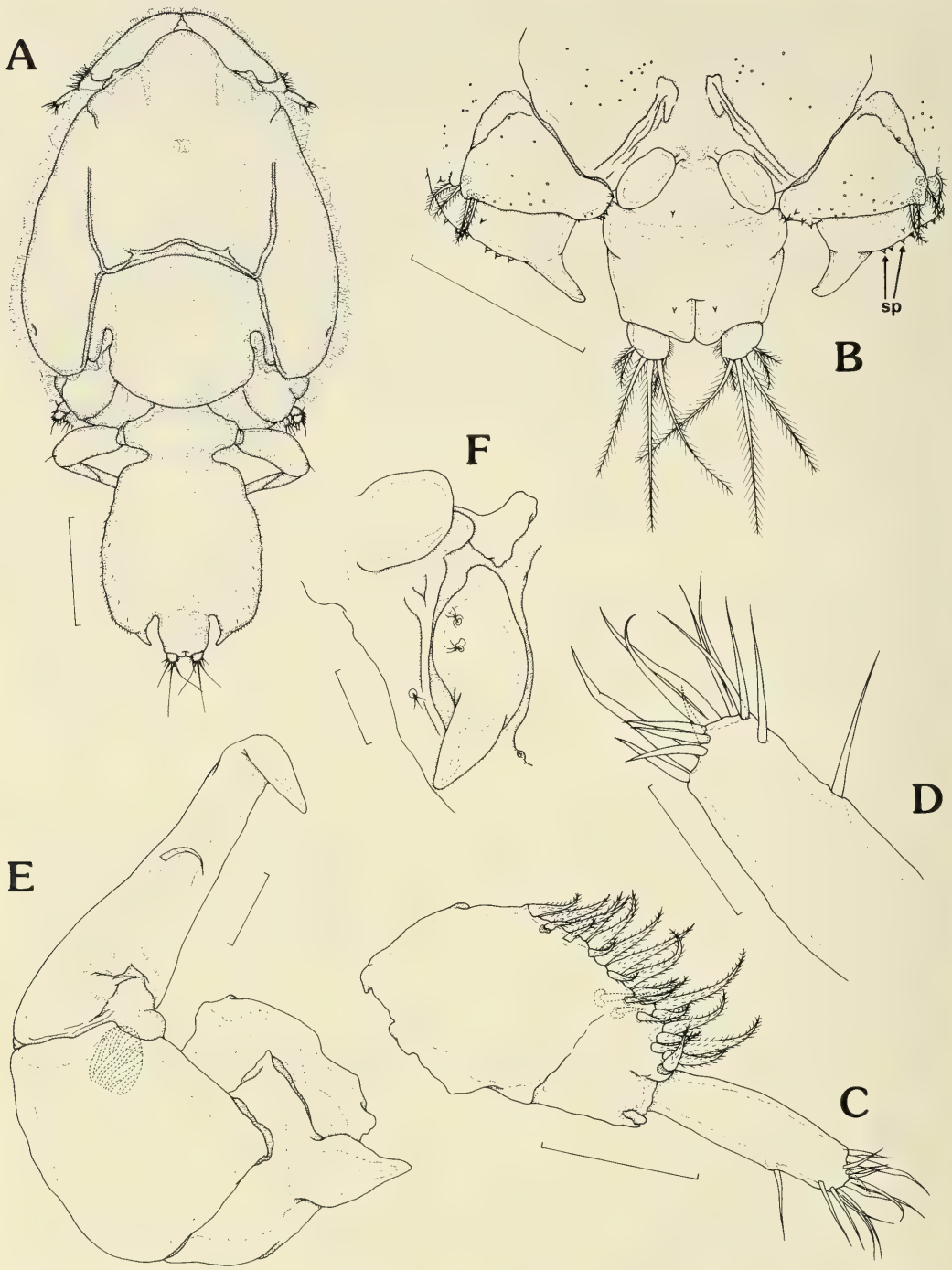


Fig. 1. *Lepeophtheirus spatha,* new species, female: A, habitus, dorsal; B, posterior portion of urosome, ventral; C, first antenna, ventral; D, tip of first antenna, ventral; E, second antenna, ventral; F, postantennal process, ventral. Symbol: sp = spinulated papillae. Scales: 1.0 mm in A; 0.5 mm in B; 0.2 mm in C; 0.1 mm in D–F.

station A7, 33°56′15″N, 118°27′28″W, in 15 m, 02 Nov 1989.

Female.—Body as in Fig. 1A. Total length (excluding setae on caudal ramus) 6.07 mm (6.02–6.16 mm) based on 3 specimens. Cephalothorax ovoid, 3.67 mm (3.62–3.77 mm) × 3.05 mm (2.96–3.16 mm). Frontal plate well-developed. Fourth pedigerous segment 3× wider than long, 0.40 mm (0.35–0.46 mm) × 1.21 mm (1.16–1.24 mm). Genital complex subquadrangular with rounded corners and convex lateral margins, longer than wide, 1.62 mm (1.52–1.70 mm) (excluding posterior process) × 1.52 mm (1.49–1.57 mm), armed with spinulated papillae on lateral margins (Fig. 1B), and bearing posterior processes. Abdomen 1-segmented, wider than long, with 2 medial pairs of setules, 0.35 mm (0.33–0.38 mm) × 0.45 mm (0.43–0.49 mm). Caudal ramus (Fig. 1B) about as long as wide, 0.10 mm (0.09–0.11 mm) × 0.11 mm (0.10–0.12 mm), and bearing 6 pinnate setae. First antenna (Fig. 1C) 2-segmented; first segment robust, with cuticular fold slightly beyond midlength, bearing 27 pilose setae (25 anteroventral and 2 dorsal setae) and 2 posterodistal spiniform processes; second segment (Fig. 1D) cylindrical, bearing 1 posterior subterminal seta and 13 terminal setae (2 sharing common base). Second antenna (Fig. 1E) 4-segmented; second segment with large, pointed, posteriorly directed, spiniform process; third segment stout, bearing usual dorsal adhesion process; terminal segment unguiform, bearing 2 setae (proximal one arising from small rounded protrusion). Postantennal process (Fig. 1F) relatively straight, stout, with 2 multibranched setules on the base and 1 lateral to it; 2 (1 large, 1 small) rounded processes anteromedial to postantennal process.

Mouth tube longer than wide, 440 × 320 μm. Mandible (Fig. 2A) of 4 parts (possibly representing segments); third and fourth parts indistinctly separated; fourth part bearing transparent membrane on lateral surface and 12 teeth on medial margin. First maxilla (Fig. 2B) consisting of papilla bearing 3 setae, and 2 flanged tines of about equal length; associated sclerotized plate armed with posterior rounded process. Second maxilla (Fig. 2C) brachiform; flabellum a striated membrane at midlength of brachium; calamus with 4 serrated membranes (only 3 illustrated in Fig. 2D); canna with 1 serrated membrane and 1 smooth one. Maxilliped (Fig. 2E) with large, rounded hyaline process on inner margin; shaft and claw partially fused on dorsal surface, but clearly separate ventrally; shaft with inner distal seta. Sternal furca (Fig. 2F) flanked on each side by slightly curved spiniform process and consisting of broad spatulate tines; each tine with wide flanges.

Leg 1 (Fig. 2G) biramous; sympod (Figs. 2G, 3A) with bifid lateral setule, 1 lateral pinnate seta (base hidden by conical process, Fig. 3A), and 1 medial pinnate seta. Exopod 2-segmented; first segment (Fig. 3B) with lateral distal corner carrying spine armed with outer row of spinules and medial margin with row of setules; second segment (Fig. 3B) with 3 spines, each spine with pectinate membranes near bases (spine 1 with minutely serrated, striated flanges; spines 2 and 3 serrated and armed with hyaline, setiform, accessory processes), 1 pinnate seta on distal medial corner, and 3 large pinnate medial setae. Endopod (Fig. 3A) vestigial, tipped with 2 setiform processes (setae?). Leg 2 (Fig. 3C) with coxa (first segment of sympod; Fig. 3D) having 1 rounded flat process and 1 conical process tipped with 1 subterminal setule near intercoxal plate, 1 lateral striated membrane, and 1 medial pinnate seta; basis with 1 naked lateral seta (Fig. 3C), 1 naked medial setule, and 1 medial striated membrane. Exopod (Fig. 3E) 3-segmented with formula I-1, I-1, II,I,5, and striated membrane on dorsal lateral margin; first exopodal spine with minutely serrated membrane at base; first and second exopodal spines with minutely serrated flanges along outer and inner margins; terminal segment with 1 spine, similar to those of first and second exopodal segments, 1

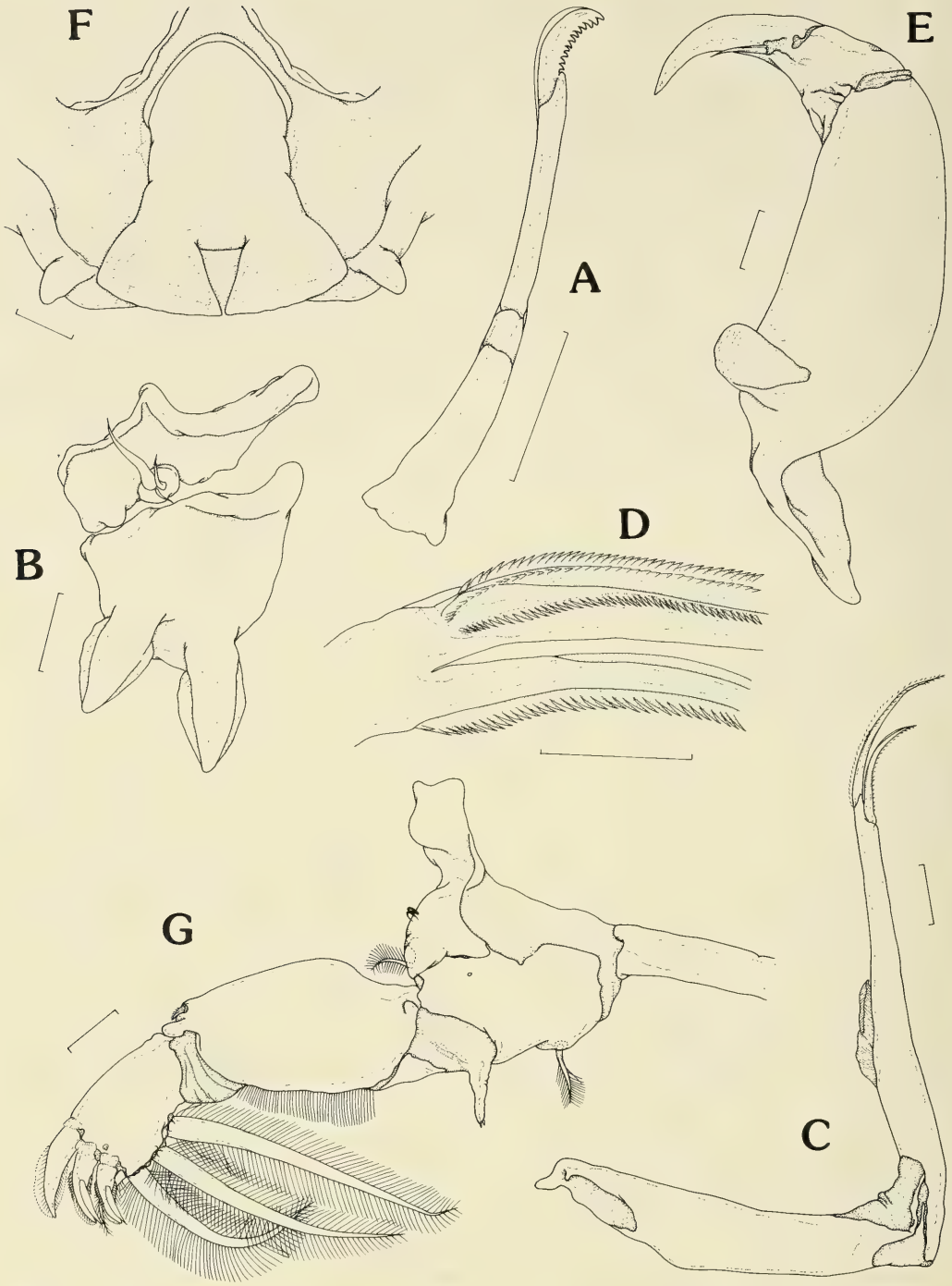


Fig. 2. *Lepeophtheirus spatha,* new species, female: A, mandible, ventral; B, first maxilla, ventral; C, second maxilla, dorsal; D, tip of second maxilla, ventral; E, maxilliped, ventral; F, sternal furca and spiniform processes, ventral; G, leg 1 and intercoxal plate, ventral. Scale: 0.1 mm in A–C, E–G; 0.05 mm in D.

curved element flanked by outer and inner transparent membranes, and 1 long setiform element with outer transparent membrane and inner row of pinnae. Endopod (Fig. 3C) with formula 0–1, 0–2, 6; first–third endopodal segments with lateral rows of setules, but only second and third segments with medial (inner) rows of setules. Leg 3 (Fig. 4A) with sympod carrying large dorsal corrugated adhesion pad, striated marginal membrane, 1 lateral pinnate seta (dorsal to insertion of exopod), 1 medial pinnate seta, and 1 large naked setule ventral to insertion of medial seta. Exopod (Fig. 4B) 3-segmented; large exopodal spine (Fig. 4C), with conspicuous lateral flanges, subterminally situated on basal swelling which carries 3 setules (dorsal one bifid) and terminal striated membrane; 1 pinnate seta (between insertion of exopod and endopod) presumably representing medial seta of first exopodal segment; second and third segments with formula I-1, III,4 (outermost seta conspicuously larger than other 3), and having rows of setules on lateral and medial margins. Endopod (Fig. 4B) 2-segmented; first segment slightly expanded laterally, with lateral row of setules and medial pinnate seta; second segment with lateral and medial rows of setules and 6 pinnate setae. Leg 4 (Fig. 4D) with sympod bearing several setules and 1 distal pinnate seta; exopod distinctly 3-segmented with formula I, I, III; each exopodal segment with outer margin bearing serrated membrane; each spine with pectinate (minutely serrated) membrane near base; spine of first exopodal segment small and naked; spine of second exopodal segment with serrated flanges; 3 spines of terminal segment (Fig. 4E) decreasing in length from inner to outer margin, with innermost spine bearing only 1 serrated flange. Leg 5 (Fig. 4F) a broad subtriangular plate with 3 pinnate setae and several papillae tipped with spinules; 1 additional pinnate seta lateral to this complex.

Male.—Body as in Fig. 5A. Total length 3.35–5.06 mm and width 1.82–2.58 mm based on 2 specimens. Cephalothorax suboval, 2.23–2.86 mm × 1.82–2.58 mm. Fourth pedigerous segment much wider than long, 0.28–0.33 mm × 0.63–0.92 mm. Genital complex wider than long, 0.52–0.59 mm × 0.79–0.90 mm. Abdomen 1-segmented, 0.23–0.37 mm × 0.29–0.43 mm. Caudal ramus armed as in female, as long as wide, 0.09–0.12 mm × 0.09–0.12 mm. Appendages as in female except those described below.

Second antenna (Fig. 5B, C) 3-segmented; first segment with 2 corrugated adhesion pads; second segment with 5 adhesion pads, distalmost pad (Fig. 5B, E) suboval and consisting of stack of lamelliform structures rimmed with striated membranes; third segment (Fig. 5D, E) curved claw with 1 hyaline seta and rounded process (Fig. 5E) on ventral surface near base, 1 seta on medial margin, and 2 longitudinal flanges on dorsal surface (Fig. 5D) and 2 on ventral surface (Fig. 5E). First maxilla (Fig. 5F) with rounded tines and 1 medial, hyaline, digitiform process; this process with subapical accessory lobe on 1 specimen examined (Fig. 5F), but accessory lobe absent on other males. Sternal furca (Fig. 5G) with blunt tips, not markedly truncate as in female.

Legs 5 and 6 (Fig. 5H) conical lobes, bearing 4 and 3 pinnate setae, respectively.

Coloration.—Live specimens are opaque, light tan with bright purple pigment concentrated along the borders of the cephalothorax and genital complex; pigmentation fades with preservation.

Etymology.—The specific name *spatha,* a Latin feminine noun meaning broad sword without point, alludes to the broad truncate tines of the sternal furca of the female; it stands as a feminine singular noun in apposition to the generic name.

Remarks.—*Lepeophtheirus spatha,* new species, can be distinguished from all its congeners by the possession of posterior processes on the genital complex of the female, the truncate sternal furcal tines, and the subtriangular leg 5 in the female.

Two species, *L. pravipes* Wilson, 1912 and *L. semicossyphi* Yamaguti, 1939 (see Ka-

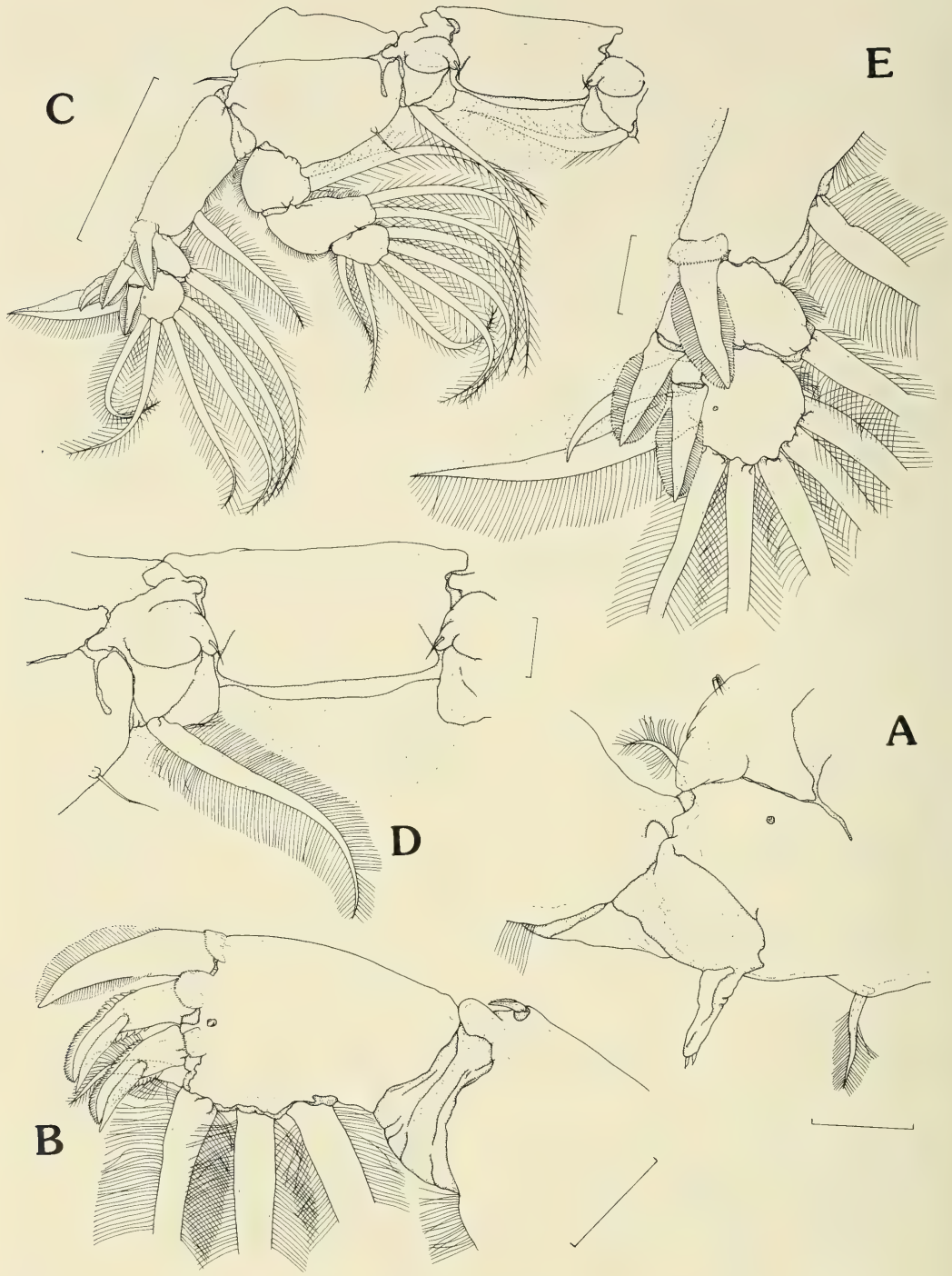


Fig. 3. *Lepeophtheirus spatha,* new species, female: A, sympod-exopod joint of leg 1, ventral; B, tip of leg 1, ventral; C, leg 2 and intercoxal plate, ventral; D intercoxal plate and proximal portion of coxa of leg 2, ventral; E, tip of leg 2 exopod, ventral. Scale: 0.1 mm in A, B, D, E; 0.5 mm in C.

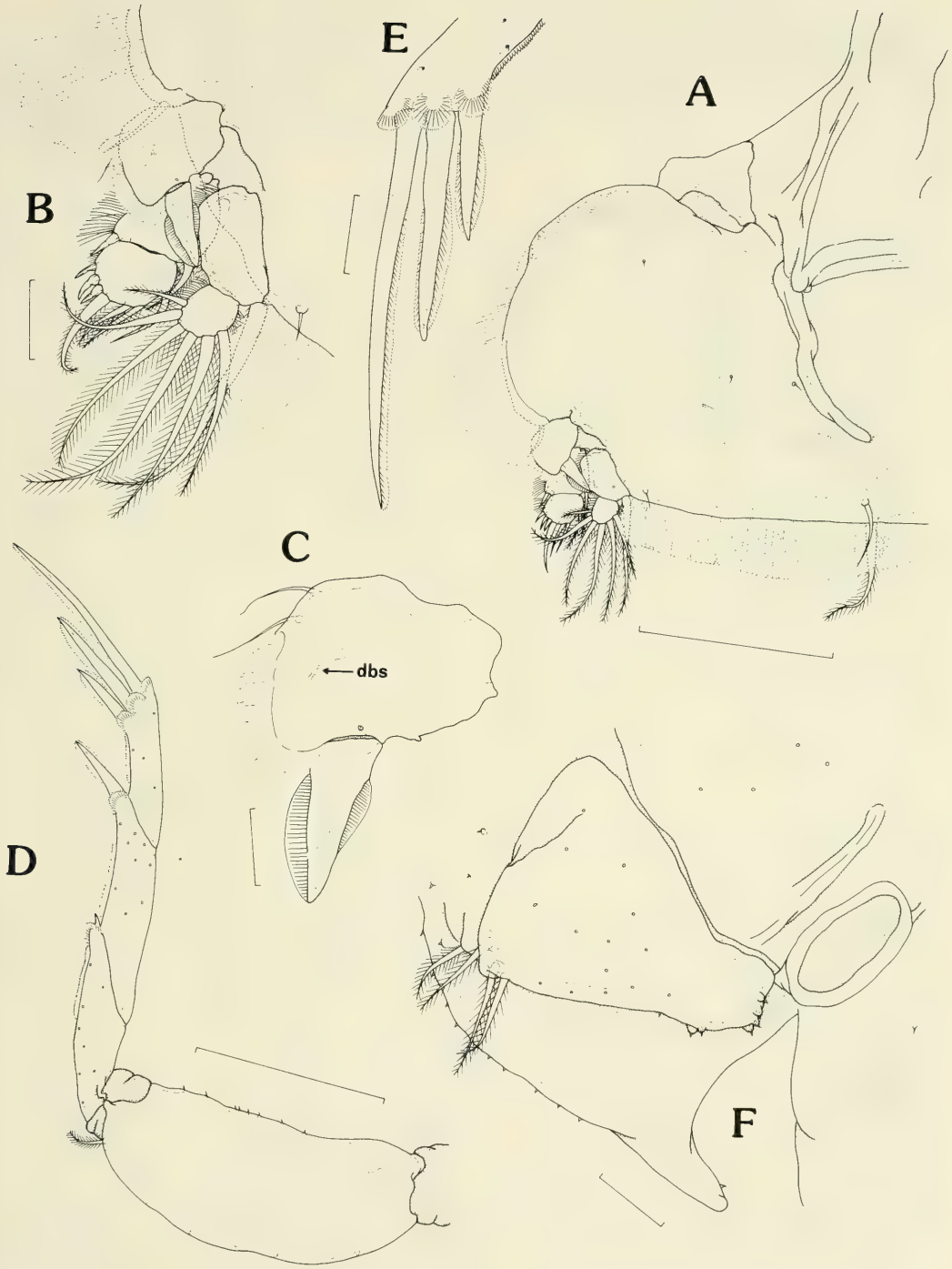


Fig. 4. *Lepeophtheirus spatha,* new species, female: A, leg 3 and ventral apron, ventral; B, leg 3, ventral; C, exopod spine of leg 3, ventral; D, leg 4, ventral; E, tip of leg 4 exopod,ventral; F, leg 5, posterior process of genital complex, and attached spermatophore, ventral. Symbol: dbs = dorsal bifid setule. Scale: 0.5 mm in A, D; 0.1 mm in B, E, F; 0.05 mm in C.

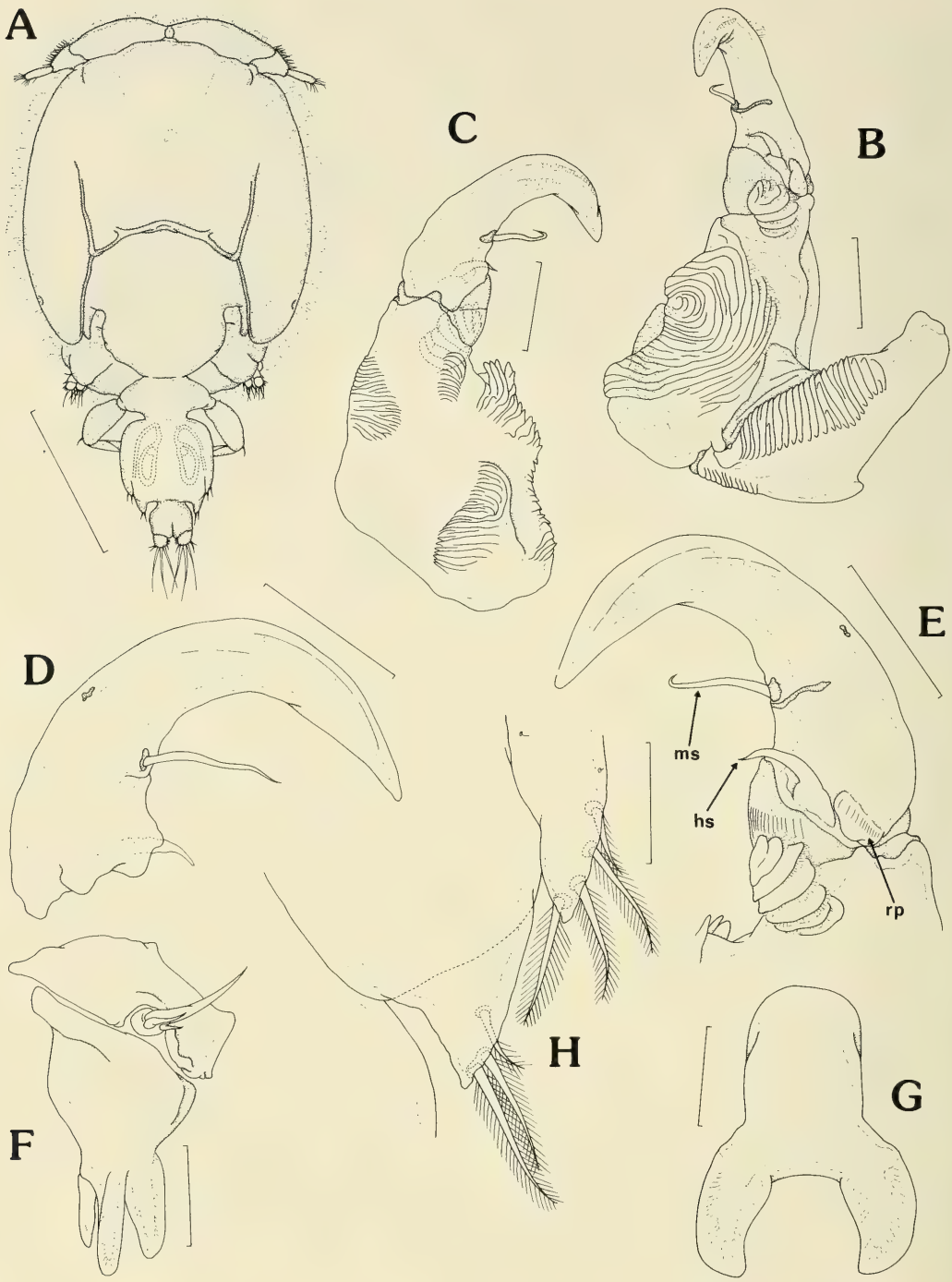


Fig. 5. *Lepeophtheirus spatha,* new species, male: A, habitus, dorsal; B, second antenna, ventral; C, distal portion of second antenna, dorsal; D, claw of second antenna, dorsolateral; E, same, ventrolateral; F, first maxilla, ventral; G, sternal furca, ventral; H, legs 5 and 6, ventral. Symbols: hs = hyaline seta; rp = rounded process; ms = medial seta. Scale: 1.0 mm in A; 0.1 mm in B–F, H; 0.2 mm in G.

bata 1974a and Shiino 1963, respectively), have a pair of posterior processes on the genital complex and a subquadrate or subtriangular leg 5 in the female as in the new species. However, *L. spatha* differs from these two species by the truncate sternal furcal tines.

The new species appears to be most closely related to *L. paralichthydis,* first described by Yamaguti & Yamasu (1960) from *Paralichthys olivaceus* (Temminck & Schlegel) from Japan. They share a similar general habitus, sternal furca, oral appendages, legs, and the very unusual, hyaline, balloon-like process on the inner margin of the base of the maxilliped of the female. This latter morphological character appears to be unique for these two species. Also, both species were collected from the external body surfaces of the halibut genus *Paralichthys.* The new species can be distinguished from *L. paralichthydis* by the presence of posterior processes on the genital complex, an attenuate basal spiniform process on the second segment of the second antenna, pointed first maxillal tines of the female, and terminal exopodal spines of leg 4 decreasing in length from the inner to the outer margin (outer two spines equal in *L. paralichthydis*).

The conical process on the inner margin of the leg 2 coxa, adjacent to the intercoxal plate, is reminiscent of that described for *L. cuneifer* Kabata, 1974 (see Kabata 1974b: 46, fig. 15). The new species, however, has a semicircular lamelliform process adjacent to this conical process on the coxa; this flat process is unique to this species.

Attempts to obtain the type specimens or newly collected material of *L. paralichthydis* for an examination of this species were futile. The type specimens could not be located and are presumably lost. Our Japanese colleagues were not able to find *L. paralichthydis* from freshly collected hosts. Apparently, this species of copepod is rare. Examination of preserved *Paralichthys olivaceus* housed in the Division of Fishes, National Museum of Natural History, Smithsonian Institution, by Smithsonian scientists also did not yield specimens of this species. A detailed redescription of *L. paralichthydis* is still needed, but could not be provided herein.

Acknowledgments

We thank Dr. R. F. Cressey, Dr. F. D. Ferrari, and Ms. P. L. Rothman, Smithsonian Institution, for examining preserved specimens of *P. olivaceus* for *L. paralichthydis* at the National Museum of Natural History, Smithsonian Institution. We are grateful to Dr. K. Izawa, Faculty of Fisheries, Mie University, Dr. K. Nagasawa, Hokkaido Fisheries Experimental Station, Dr. I. Takeuchi, Otsuchi Marine Research Center, University of Tokyo, and Dr. S. Uye, Faculty of Applied Biological Science, Hiroshima University for attempting to obtain new specimens of *L. paralichthydis.* This study was partially funded by grant number 91-1 from the Southern California Association of Marine Invertebrate Taxonomists and is contribution number 4 of this association.

Literature Cited

Humes, A. G., & R. U. Gooding. 1964. A method for studying the external anatomy of copepods.—Crustaceana 6:238–240.

Kabata, Z. 1974a. The species of *Lepeophtheirus* (Copepoda: Caligidae) from fishes of British Columbia.—Journal of the Fisheries Research Board of Canada 30:729–759.

———. 1974b. *Lepeophtheirus cuneifer* sp. nov. (Copepoda: Caligidae), a parasite of fishes from the Pacific coast of North America.—Journal of the Fisheries Research Board of Canada 31:43–47.

Shiino, S. M. 1963. Note on *Lepeophtheirus semicossyphi* Yamaguti (Copepoda: Caligoida).—Publications of the Seto Marine Biological Laboratory 11:409–414.

Yamaguti, S., & T. Yamasu. 1960. New parasitic copepods from Japanese fishes.—Publications of the Seto Marine Biological Laboratory 8:141–152.

Environmental Monitoring Division, Hyperion Treatment Plant, 12000 Vista del Mar, Playa del Rey, California 90293, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 736–741

THE STILLMAN WRIGHT COLLECTION OF COPEPODA (CRUSTACEA) FROM SOUTH AMERICA IN THE NATIONAL MUSEUM OF NATURAL HISTORY, SMITHSONIAN INSTITUTION

Janet W. Reid

Abstract.—The species of Calanoida and Cyclopoida (Copepoda: Crustacea) from South America that were deposited by Stillman Wright in the collections of the National Museum of Natural History are listed. The collection includes type specimens of 8 species and specimens from type localities of 5 additional species of Diaptomidae from Brazil. These deposits and others in the Kiefer Collection in Germany represent the only known surviving material from Wright's taxonomic studies of South American Calanoida. Previously unpublished records of several species from the collection are listed.

During his career, the American limnologist Stillman Wright described 29 species and subspecies of calanoid copepods of the families Boeckellidae, Diaptomidae, and Pseudodiaptomidae. Most of these species were from inland Brazil and Argentina, and a few were from marine and freshwater collections in Nigeria and the Philippines (Wright 1927–1939, Wright & Tressler 1928). Wright also redescribed 18 species of calanoids from inland and coastal waters of Brazil (Wright 1927, 1928a), and reported on collections from Argentina (Wright 1939). These articles are among the fundamental early works on South American continental Calanoida, and the material that Wright described constitutes a basic resource for continuing taxonomic studies of these zooplankters. The present article lists type and non-type specimens of Copepoda of the Wright Collection held in the National Museum of Natural History, Smithsonian Institution. This collection apparently represents most of the surviving material from Wright's work.

Most of the species described by Wright are still considered valid, a measure of the care and thoroughness of his work. In a review of the known distribution and current nomenclature of South American diaptomids, Brandorff (1976) listed only *Diaptomus* (now *Calodiaptomus*) *merrillae* and *D. perelegans* Wright, 1927, as possibly belonging to one variable species, a question still unresolved. In addition, both Brandorff (in Brandorff et al. 1982) and Dussart (1984) suggested that the female originally described as that of *Diaptomus* (now *Dactylodiaptomus*) *pearsei* Wright, 1927, is not the same species as the male. These authors furnished descriptions of similar but not identical females ascribed to *D. pearsei* from the Amazon and Orinoco rivers, respectively. A full listing of works treating Wright's species is beyond the scope of this article; readers are referred to the article by Brandorff (1976) for an indispensable introduction to the literature on South American diaptomids.

Wright drew on two sources of material. His earlier articles treated the calanoids from a collection made by Miss Harriet Merrill from the Amazon Basin and other localities in South America in 1907 and 1908. This collection was acquired by Dr. Chancey Juday and formed the basis for part of Wright's doctoral dissertation (Wright 1928a), which was published as a general revision of South

American Diaptomidae (Wright 1927). Later articles (Wright 1935, 1936a, 1936b, 1938a, 1938b) described material collected by Wright himself in his capacity as staff limnologist of a fisheries project directed by Dr. Rodolfo Von Ihering in the Brazilian northeast. During Wright's stay in Brazil (1933–1937), he also collected in southeastern Brazil and northern Argentina (Reid 1989; Wright 1937a, 1937b, 1939).

The Merrill Collection cannot now be located at the University of Wisconsin (S. Dodson, letter to J. Reid, 1991; J. Lyons, letter to S. Wright, 1985). Some Brazilian copepods were deposited by Wright in the U.S. National Museum (USNM), later the National Museum of Natural History (NMNH) in 1926, before his own sojourn in South America. It can be assumed that these specimens came from the Merrill Collection. This material includes all species in Table 1 and, in Table 2, the specimens originally deposited as *D. henseni,* a species that Wright himself later redescribed as *D. amazonicus* (Wright 1935). Additional non-type material of species that were described by Wright in the 1927 article and deposited later may also have been part of the Merrill Collection, although she is not listed as the collector of any of these samples. This supposition is largely an inference from the incomplete and sometimes misspelled locality and date information supplied with the specimens, which is uncharacteristic of Wright's later work, and from the fact that some specimens are listed from localities that were never visited by Wright but were sampled by Merrill. Specimens in this category include, from Table 2: *Diaptomus coniferoides,* USNM 92947; *D. flexipes,* USNM 92953; *D. pearsei,* USNM 92949, 92950; *D. perelegans,* USNM 92951; *D. silvaticus infrequens,* USNM 92952; and *Pseudodiaptomus gracilis,* USNM 60599, 60600, 92945. If this supposition is correct, the slides of *D. pearsei,* although they were not listed as type material at time of deposit, come from the type locality of the species and were probably used by Wright in his original description. Designated type material of *D. pearsei* is no longer in existence (Table 3).

Table 1.—Type specimens of South American Diaptomidae (Calanoida) described by Wright and deposited in the collections of the National Museum of Natural History, Smithsonian Institution.

Diaptomus coniferoides Wright, 1927. USNM 59827, Type ♂, ALC, Calama, Brazil, no date. USNM 59828, Paratype ♀, ALC, Calama, Brazil, no date. (*Notodiaptomus*)

Diaptomus flexipes Wright, 1927. USNM 59818, Type ♂, ALC, Santarém, Brazil, no date. USNM 59819, Paratype ♀, ALC, Santarém, Brazil, no date. (*Rhacodiaptomus*)

Diaptomus insolitus Wright, 1927. USNM 59474, Type ♂, ALC, Calama, Amazonas, Brazil, no date. USNM 59475, Paratype ♀, ALC, Calama, Amazonas, Brazil, no date. (*Rhacodiaptomus*)

Diaptomus merrillae Wright, 1927. USNM 59510, Type ♂, ALC, Calama, Amazonas, Brazil, no date. USNM 59511, Paratype ♀, ALC, Calama, Amazonas, Brazil, no date. (*Calodiaptomus*)

Diaptomus perelegans Wright, 1927. USNM 59512, Type ♂, ALC, Calama, Amazonas, Brazil, no date. USNM 59513, Paratype ♀, ALC, Calama, Amazonas, Brazil, 17 May 1926. (*Calodiaptomus*)

Diaptomus santaremensis Wright, 1927. USNM 59514, Type ♀, ALC, Santarém, Grao Para, Brazil, no date. (*Diaptomus* s. l.)

Diaptomus silvaticus Wright, 1927. USNM 59822, Type ♂, SLI, Para, Brazil, no date. USNM 59823, Paratype ♀, ALC, Para, Brazil, no date. (*Diaptomus* s.l.)

Diaptomus silvaticus infrequens Wright, 1927. USNM 59824, Type ♂, SLI, Para, Brazil, no date. (*Diaptomus* s. l.)

Regarding material collected during his own stay in Brazil, Wright once (1935:214) indicated that specimens were to be deposited at the Museu Nacional, Rio de Janeiro, Brazil, at the Museum of Zoology of the University of Michigan, and at the U.S. National Museum. However, the Museu Nacional presently holds no material deposited by Wright (M. M. G. Corrêa, letter to J. Reid, 1989), and all collections of Crustacea held by the Museum of Zoology were transferred to the NMNH in the 1930's (M. O'Brien, pers. comm. to J. Reid, 1989).

Table 2.—Non-type specimens of South American Calanoida and Cyclopoida from the Wright Collection in the National Museum of Natural History, Smithsonian Institution.

Calanoida: Boeckellidae

Boeckella bergi Richard, 1897. USNM 79546, 50+, ALC, Laguna in Plátano, between Buenos Aires and La Plata, Argentina, 5 Jan 1937 (includes *Acanthocyclops vernalis*). USNM 92965, 28, ALC, roadside pool, Guamini, Prov. Buenos Aires, Argentina, 10 Jan 1937. USNM 92968, 1000+, L. en Platano, near Quilmes, Argentina, 6 Jan 1937 (includes *A. vernalis*); det. J. W. Reid.

Boeckella dentifera Brehm, 1935. USNM 79545, 50+, ALC, Laguna Salada at La Dulce, Prov. Buenos Aires, Argentina, 18 Jan 1937.

Boeckella gracilis Daday, 1901. USNM 79547, 50+, ALC, Laguna Sarco, near Lavaisse, Prov. San Luis, Argentina, 10 Dec 1936. USNM 92956, 100+, ALC, L. Encadenada, Esta, San Luis, Argentina, 9 Dec 1936 (includes *B. poopoensis*). USNM 92957, 200+, ALC, Lago Chascomus, Argentina, 9 Nov 1936. USNM 92958, 200+, ALC, L. Sarco, San Luis, Argentina, 10 Dec 1936. USNM 92959, 200+, ALC, L. Alvardon Deffarrari, Argentina, 18 Jan 1937. USNM 92966, 1000+, ALC, Tres Lagunas, Argentina, No. 2, 5 Dec 1936 (includes *Mesocyclops annulatus* and *Metacyclops mendocinus*); det. J. W. Reid. USNM 92967, 1000+, ALC, Tres Lagunas, Argentina, No. 2, 5 Dec 1936 (includes *M. annulatus* and *M. mendocinus*); det. J. W. Reid. USNM 92969, 10+, ALC, L. Nassau, San Luis, Argentina, 7 Dec 1936 (includes *Diaptomus incompositus* and *M. mendocinus*); det. J. W. Reid.

Boeckella poopoensis Marsh, 1906. USNM 79548, 50+, ALC, Laguna Alsina, near Bonafacio, Prov. Buenos Aires, Argentina, 10 Jan 1937.

Calanoida: Diaptomidae

Diaptomus amazonicus Wright, 1935. USNM 59515, 1 ♂, ALC, Lake Arary, Marojo (sic), Brazil, no date. USNM 59817, 1 ♀, ALC, Lake Arary, Marojo (sic), Brazil, no date. USNM 79541, 2 ♂, ALC, Marajó Island, Pará, Brazil, "from type locality," no date. (USNM 59515 and 59817 were originally deposited as *D. henseni* Dahl, 1894; these determinations were later changed and the species described as *D. amazonicus* by Wright, 1935.) (*Notodiaptomus*)

Diaptomus anisitsi Daday, 1905. USNM 92971, 50+, ALC, L. Cricket Club, Buenos Aires, Argentina, 1 Jan 1936. (*Notodiaptomus*)

Diaptomus azevedoi Wright, 1935. USNM 79544, 7, ALC, açude (artificial lake) near São João do Rio do Peixe, Parahyba, Brazil, "from type locality," no date. (*Argyrodiaptomus*)

Table 2.—Continued.

Diaptomus bergi Richard, 1897. USNM 92954, 1 ♂, SLI, Guamini, Buenos Aires, Argentina, no date. USNM 92955, 1 ♂, SLI, Guamini, Buenos Aires, Argentina, no date. USNM 92964, 300+, ALC, Glew, Prov. Buenos Aires, Argentina, 26 Dec 1936. (*Argyrodiaptomus*)

Diaptomus coniferoides Wright, 1927. USNM 92947, 1 ♂, SLI, Brazil, no date. USNM 92962, 200+, ALC, Arroyo Pajarito, Tigré, Argentina, 30 Nov 1936 (includes *Pseudodiaptomus richardi* Dahl). USNM 92963, 20+, ALC, Rio Terito, near Tigré, Argentina, 26 Nov 1936 (includes *Pseudodiaptomus richardi* Dahl). (*Notodiaptomus*)

Diaptomus flexipes Wright, 1927. USNM 92953, 1 ♂, SLI, Santarém, Brazil, no date. (*Rhacodiaptomus*)

Diaptomus iheringi Wright, 1935. USNM 79542, 7+, ALC, Açude Puxinanã, near Campina Grande, Parahyba, Brazil, "type locality," no date. (*Notodiaptomus*)

Diaptomus incompositus Brian, 1926. USNM 92960, 100+, ALC, lago artificial, Balneario, Quilmes, Argentina, 1 Jan 1937. USNM 92961, 300+, ALC, Lago Chascomus, Argentina, 10 Nov 1936. USNM 92970, 1000+, ALC, Tres Lagunas, San Luis, Argentina, 5 Dec 1936 (includes *Eucyclops neumani* and *M. mendocinus*); det. J. W. Reid. USNM 250913, 6 ♀, 4 ♂, ALC, L. Nassau, San Luis, Argentina, 7 Dec 1936 (out of USNM 92969); det. J. W. Reid. (*Notodiaptomus*)

Diaptomus nordestinus Wright, 1935. USNM 79543, 5+, ALC, Açude Simão, near Campina Grande, Parahyba, Brazil, "from type locality," no date. (*Notodiaptomus*)

Diaptomus pearsei Wright, 1927. USNM 92949, 1 ♂, SLI, Calama, Brazil, no date. USNM 92950, 1 ♀, SLI, Calama, Brazil, no date. (*Dactylodiaptomus*)

Diaptomus perelegans Wright, 1927. USNM 92951, 1 ♂, SLI, Brazil (word "Para" on label crossed out), no date. (*Calodiaptomus*)

Diaptomus silvaticus infrequens Wright, 1927. USNM 92952, 1 ♂, SLI, Para, Brazil, no date. (*Diaptomus* s. l.)

Diaptomus transitans Kiefer, 1929. USNM 92972, 100+, ALC, Emb. S. Roque, Rio Primero, Argentina, 21 Dec 1936. (*Notodiaptomus*)

Calanoida: Pseudodiaptomidae

Pseudodiaptomus gracilis (Dahl, 1894). USNM 60599, 1 ♂, ALC, South America, no date. USNM 60600, 1 ♀, ALC, South America, no date. USNM 92945, 1 ♀, SLI, South America, no date.

Pseudodiaptomus richardi (Dahl, 1894). USNM 92963, 4 ♀, 5 ♂, ALC, Rio Terito near Tigré, Argentina, 26 Nov 1936. USNM 233581, 9 ♂, 21 ♀, ALC, lago

Table 2.—Continued.

artificial, Balneario, Quilmes, Argentina, 1 Jan 1937 (out of USNM 92960); det. T. C. Walter.

Cyclopoida: Cyclopidae

Acanthocyclops vernalis (Fischer, 1853). USNM 250911, 3 ♀, 3 ♂, ALC, L. en Platano, near Quilmes, Argentina, 6 Jan 1937 (out of USNM 92968); det. J. W. Reid. USNM 250916, 50+, ALC, Laguna in Plátano near Buenos Aires, Argentina, 5 Jan 1937 (out of USNM 79546); det. J. W. Reid.

Eucyclops neumani (Pesta, 1927). USNM 250908, 3 ♀, 5 ♂, 2 copepodids, ALC, Tres Lagunas, San Luis, Argentina, 5 Dec 1936 (out of USNM 92970); det. J. W. Reid.

Mesocyclops annulatus (Wierzejski, 1892). USNM 250915, 38, roadside pool, Guamini, Prov. Buenos Aires, Argentina, 10 Jan 1937 (out of USNM 92965); det. J. W. Reid. USNM 250919, 100+, ALC, Tres Lagunas, Argentina, No. 2, 5 Dec 1986 (out of USNM 92966); det. J. W. Reid.

Metacyclops mendocinus (Wierzejski, 1892). USNM 250910, 2 ♀, ALC, Tres Lagunas, Argentina, No. 2, 5 Dec 1936 (out of USNM 92966); det. J. W. Reid. USNM 250912, 4 ♀, 3 ♂, ALC, L. Nassau, San Luis, Argentina, 7 Dec 1936 (out of USNM 92969); det. J. W. Reid. USNM 250907, 2 ♀, 4 ♂, ALC, Tres Lagunas, San Luis, Argentina, 5 Dec 1936 (out of USNM 92970); det. J. W. Reid.

Wright himself (pers. comm. to J. Reid, 1985) did not recall having made deposits in any museum except the NMNH. Wright did send a few samples from Brazil to Dr. Friedrich Kiefer. These specimens are now held in the Kiefer Collection at the Staatliches Museum für Naturkunde Karlsruhe in Germany (Franke 1989:138, 293). All material, including unsorted plankton samples, that was in Wright's possession upon his return to the United States was eventually deposited in the collections of the Division of Crustacea, Department of Invertebrate Zoology, NMNH. The holdings at NMNH and in the Kiefer Collection therefore appear to represent the only South American material described or collected by Wright that is still in existence. Specimens deposited by Wright from other parts of the world are also held by the NMNH. Wright's field notes from the Brazil years are deposited in the archives of the C. B. Wilson Copepod Library, NMNH.

Table 1 lists those of Wright's type specimens of South American Diaptomidae that are held by the NMNH, together with catalog number, type status, method of preservation, and locality data. Table 2 lists additional, non-type South American material of Calanoida and Cyclopoida that was donated by Wright to the NMNH collections. All species were determined by Wright himself unless otherwise indicated. Some of the Brazilian specimens listed in Table 2 are labeled "from type locality" according to information given by Wright at the time of deposit. Most other specimens of Diaptomidae are from localities that were mentioned by Wright in one or more articles, although some of these localities and all the localities of *Boeckella* spp. represent previously unpublished records. Some of the material is from unsorted plankton samples that were labeled according to the dominant genus at the time of deposit, and were recently examined by myself. These determinations are indicated in Table 2 and also represent new records. Records of *Pseudodiaptomus* spp. were published in detail by Walter (1989). The method of preservation is indicated by ALC (alcohol) or SLI (slide). Locality names follow the spelling on the labels; modern Portuguese spelling is quite different in some cases. Genera of the Family Diaptomidae have undergone several revisions; species are listed under the original genus name, *Diaptomus,* with the presently accepted genus name appended in parentheses.

Table 3 lists species described by Wright for which original type material is apparently no longer in existence. The type locality or, if no type locality was specified in the original article, all the localities mentioned are given. The present genus name is given in parentheses.

Table 3.—Species of South American Diaptomidae and Pseudodiaptomidae described by Wright for which type material apparently no longer exists.

Diaptomus amazonicus Wright, 1935. No type locality specified. Localities mentioned in original description: Rio Tapajoz near Santarém, Lago Arary, Island of Marajó, Rio Arama, all in Pará, Brazil; Essequibo River and at Georgetown, British Guiana. (*Notodiaptomus*)

Diaptomus argentinus Wright, 1938b. Type locality: pool 3 km south of Glew, on the road to San Vicente, Buenos Aires Province, Argentina. (*Argyrodiaptomus*)

Diaptomus azevedoi Wright, 1935. Type locality: small açude on sitio Olho d'Agua, near Açude Pilões, Parahyba, Brazil. (*Argyrodiaptomus*)

Diaptomus calamensis Wright, 1927. No type locality specified. Localities mentioned in original description: Calama, Amazonas, and Santarem, Grao Para, Brazil. (*Rhacodiaptomus*)

Diaptomus cearensis Wright, 1936b. No type locality specified. Localities mentioned in original description: northeastern Ceará, Açude Pilões, near São João do Rio do Peixe, Parahyba; several waters near Caraúbas and Assú, Rio Grande do Norte, Brazil. (*Notodiaptomus*)

Diaptomus corderoi Wright, 1936b. Type locality: Lagoa Santa near Bello Horizonte, Minas Geraes, Brazil. Topotype material has been deposited at NMNH and at the Museu de Zoologia da Universidade de São Paulo (Reid 1987). (*Scolodiaptomus*)

Diaptomus dahli Wright, 1936b. Type locality: Rio Arary, Marajó Island, Pará, Brazil. (*Notodiaptomus*)

Diaptomus iheringi Wright, 1935. Type locality: Açude Puxinanã, village of Puxinanã, near Campina Grande, Parahyba, Brazil. (*Notodiaptomus*)

Diaptomus isabelae Wright, 1936b. No type locality specified. Localities mentioned in original description: two pools near Jatobá, Pernambuco, Brazil. (*Notodiaptomus*)

Diaptomus jatobensis Wright, 1936b. Type locality: pool at Itaparica Falls, Bahia side of Rio São Francisco, near Jatobá, Pernambuco, Brazil. (*Notodiaptomus*)

Diaptomus neglectus Wright, 1938b. Type locality: pool at Jaguára, near Bello Horizonte, Minas Geraes, Brazil. (*Argyrodiaptomus*)

Diaptomus nordestinus Wright, 1935. No type locality specified. Localities mentioned in original description: Açude Simão and pool, both near Campina Grande, and Açudes Linda Flor and Lapa, Parahyba, Brazil. (*Notodiaptomus*)

Diaptomus paulistanus Wright, 1936b. No type locality specified. Localities mentioned in original description: five waters near São Paulo, and one in Juiz de Fóra, Minas Geraes, Brazil. (*Odontodiaptomus*)

Table 3.—Continued.

Diaptomus pearsei Wright, 1927. Type locality: South Pond, Calama, Amazonas, Brazil. (*Dactylodiaptomus*)

Pseudodiaptomus marshi Wright, 1936a. Type locality: Rio Capibaribe, Recife, Brazil.

Acknowledgments

I am grateful to Drs. Stanley Dodson, John Lyons, and Edward Schneberger, and most especially to the late Dr. Stillman Wright for their assistance in attempting to locate the Merrill Collection at the University of Wisconsin and its Zoological Museum. Dr. Mark O'Brien verified the transfer of Crustacea from the collections of the Museum of Zoology of the University of Michigan to the NMNH. Dra. Maria Margarida Gomes Corrêa of the Museu Nacional da Universidade Federal do Rio de Janeiro obligingly searched the collections of that institution for material deposited by Dr. Wright. Two anonymous reviewers provided helpful comments.

Literature Cited

Brandorff, G.-O. 1976. The geographic distribution of the Diaptomidae in South America (Crustacea, Copepoda).—Revista Brasileira de Biologia 36(3):613–627.

———, W. Koste, & N. N. Smirnov. 1982. The composition and structure of rotiferan and crustacean communities of the lower Rio Nhamundá, Amazonas, Brazil.—Studies on Neotropical Fauna and Environment 17:69–121.

Dussart, B. H. 1984. Some Crustacea Copepoda from Venezuela.—Hydrobiologia 113:25–67.

Franke, U. 1989. Katalog zur Sammlung limnischer Copepoden von Prof. Dr. Friedrich Kiefer.—Carolinea, Staatliches Museum für Naturkunde Karlsruhe 5:1–433.

Reid, J. W. 1987. *Scolodiaptomus,* a new genus proposed for *Diaptomus* s. l. *corderoi* Wright; and description of *Notodiaptomus brandorffi,* new species (Copepoda; Calanoida), from Brazil.—Journal of Crustacean Biology 7(2):364–379.

———. 1989. Stillman Wright (1898–1989).—Journal of Crustacean Biology 9(4):680–683.

Walter, T. C. 1989. Review of the New World species

of *Pseudodiaptomus* (Copepoda: Calanoida) with a key to the species.—Bulletin of Marine Science 45(3):590–628.

Wright, S. 1927. A revision of the South American species of *Diaptomus*.—Transactions of the American Microscopical Society 46(2):73–121.

———. 1928a. Studies in aquatic biology. I. A chemical and plankton study of Lake Wingra. II. A revision of the South American species of *Diaptomus*. III. A contribution to the knowledge of the genus *Pseudodiaptomus*. Unpublished Ph.D. Thesis, University of Wisconsin.

———. 1928b. A new species of *Diaptomus* from the Philippine Islands.—Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 23:583–585, Plate 11.

———. 1928c. A contribution to the knowledge of the genus *Pseudodiaptomus*.—Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 23:587–600.

———. 1935. Three new species of *Diaptomus* from northeast Brazil.—Annaes da Academia Brasileira de Sciencias 7(3):213–233 + Plates I–IV.

———. 1936a. A revision of the South American species of *Pseudodiaptomus*.—Annaes da Academia Brasileira de Sciencias 8(1):1–24 + Plates I–III.

———. 1936b. Preliminary report on six new species of *Diaptomus* from Brazil.—Annaes da Academia Brasileira de Sciencias 8(2):79–85 + Plates I, II.

———. 1937a. A review of some species of *Diaptomus* from São Paulo.—Annaes da Academia Brasileira de Sciencias 9(1):65–82 + Plates I–III.

———. 1937b. Two new species of *Pseudodiaptomus*.—Annaes da Academia Brasileira de Sciencias 9(1):155–162 + Plates I, II.

———. 1938a. Distribuição geographica das especies de *Diaptomus* na America do Sul.—Livro Jubilar do Prof. Travassos, Rio de Janeiro 3:561–566 + Plate I.

———. 1938b. A review of the *Diaptomus bergi* group, with descriptions of two new species.—Transactions of the American Microscopical Society 57(3):297–315.

———. 1939. Algunas especies del género "Diaptomus" (Copepoda-Calanoida) halladas en la República Argentina.—Physis, Buenos Aires 17: 645–649.

———, & W. L. Tressler. 1928. Two new species of *Diaptomus* from Nigeria.—Transactions of the American Microscopical Society 47(3):372–377.

Department of Invertebrate Zoology, NHB-163, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 742–750

V. L. WAGIN'S COLLECTIONS OF DENDROGASTRIDAE (CRUSTACEA: ASCOTHORACIDA) IN THE U.S.S.R., WITH DESIGNATIONS OF LECTOTYPES

Mark J. Grygier

Abstract.—An inventory is given of the echinoderm-parasitizing dendrogastrid Ascothoracida studied by V. L. Wagin that are housed in the Zoological Institute, U.S.S.R. Academy of Sciences, and the Department of Invertebrate Zoology, Leningrad University. Complete locality data for most of these Arctic and boreal Pacific species are given for the first time. Lectotypes are designated for one species of *Ulophysema* and eight species of *Dendrogaster,* and the asteroid hosts of *D. astericola, D. dogieli,* and *D. beringensis* are reidentified as *Henricia skorikovi, Pteraster octaster,* and *Eremicaster crassus,* respectively.

Резюме.—Описана коллекция дендрогастрид (Ascothoracida) - паразитов иглокожих, изученная В. Л. Вагиным, которая хранится в Зоологическом институте Академии наук СССР и на кафедре Зоологии беспозвоночных Ленинградского государственного университета. Приводится впервые полный список местонахождений для большинства из этих арктических и бореальных тихоокеанских видов. Выделены лектотипы для одново из видов *Ulophysema* и восьми видов *Dendrogaster.* Морские звезды-хозяева *D. astericola, D. dogieli* и *D. beringensis* переопределены как *Henricia skorikovi, Pteraster octaster* и *Eremicaster crassus,* соотвественно.

The Dendrogastridae include three genera of crustacean endoparasites of echinoderms (Grygier 1987). Wagin (1950b, 1957, 1976) conducted taxonomic studies of 13 species of *Dendrogaster* infesting Asteroidea, mostly from the vicinity of Sakhalin and the western Bering Sea, and he published one record (Wagin 1964) of echinoid-infesting, Arctic *Ulophysema.* The Pacific specimens were collected by A. V. Ivanov in 1931 and 1932 and by Wagin himself in 1947 and 1950. Wagin's publications were usually unspecific about collection data and deposition of specimens, often mentioning only the year, station number, and host, and he never designated any primary types. Two partial compilations of Wagin's findings (Lindberg 1959, Barel & Kramers 1977) did little to clarify matters. The following is an inventory of the extant material of each species in Leningrad and its condition, with full locality data and lectotype designations in most cases.

Materials.—In 1985 I examined the type lot of *Ulophysema pourtalesiae* Brattström in the Zoologisk Museum in Copenhagen and borrowed specimens of *Dendrogaster astericola* Knipowitsch and *D. murmanensis* Wagin from the Zoological Institute (ZIN) in Leningrad. During a visit to the ZIN in 1989 I was able to examine abundant catalogued material of *Dendrogaster,* as well as uncatalogued specimens that had been transferred from Kazan University after Wagin's death in 1984. All of the pertinent species of *Dendrogaster* were represented and I could match many specimens with Wagin's illustrations; the glass-plate negatives of Wagin's (1950b) photographs were also present. However, some specimens and almost all of Wagin's microscopical preparations were missing. At Leningrad Uni-

versity (LGU), where Wagin did his graduate work, there were some specimens in the teaching collection of the Department of Invertebrate Zoology and a few slides in the parasitological collection. Efforts to determine whether there are any specimens in the Zoological Museum of Moscow University have been fruitless. A. V. Smirnov of the ZIN, after searching station lists (e.g., Ivanov 1933) and consulting with A. V. Ivanov and G. M. Belyaev, was able to provide me with almost all the detailed collection data pertaining to the Pacific *Dendrogaster* and Arctic *Ulophysema* samples (Appendix).

Several of Wagin's specific names appeared first as nomina nuda (e.g., Korschelt 1933; Vaghin (=Wagin) 1946; Wagin 1948a, 1948b), sometimes under varying spellings, and some of the spellings employed here are corrected to conform to the International Code of Zoological Nomenclature. It is possible that some of the new specific names accompanied by extremely brief characterizations in Wagin's (1950a) dissertation summary, which preceded the full descriptions (Wagin 1950b) by several months, meet the criteria of publication and availability, though I provisionally consider them nomina nuda; the spellings of two specific names were different in the earlier work (see below). Since Wagin did not designate primary types, I am treating as syntypes all female and male specimens in the samples that were mentioned in his original descriptions.

Genus *Ulophysema* Brattström, 1936
Ulophysema pourtalesiae Brattström, 1937

This endoparasite of the irregular echinoid *Pourtalesia jeffreysi* Wyville Thomson was originally described from bathyal depths between Greenland and the Norwegian Slope. Wagin (1964, 1976) reported it from the northern Kara Sea, implying but not specifying that it had the same host. I did not find Wagin's material in Leningrad in 1989, but I am taking this opportunity to name one of Brattström's syntypes in the Zoologisk Museum in Copenhagen as the lectotype. This is the female from host #7 in the type lot. Its isolated body has been illustrated (Brattström 1937:fig. 3), and its carapace (mantle) is torn into two pieces. It was collected at the type locality designated by Brattström: Danish Three-Year Expedition to East Greenland, sta. 96, 13 Aug 1932, off Cape Franklin in the Franz Josef Fjord, East Greenland 73°15′N, 22°30′W, 325 m, 1.5°C.

Genus *Dendrogaster* Knipowitsch, 1890
Dendrogaster astericola
Knipowitsch, 1890

This is the type species of the genus. The original description was based on two females from the Solovetskiy Islands in the White Sea, a brooding one infesting *Henricia sanguinolenta* (O. F. Müller) and a nonbrooding one infesting *Solaster endeca* (L.); the host names are as given by Knipowitsch (1892). The first specimen, collected by Knipowitsch himself, is housed in the ZIN (1/19631, 2/19632), but only a lobe of the mantle, some brooded ascothoracid-larvae, and the host asteroid are preserved. This is an illustrated specimen (Knipowitsch 1891: fig. 2, 1892:taf. I, figs. 1, 2) and I am choosing it as the lectotype. The second specimen has been reidentified as *D. murmanensis* by Wagin (1950b; see below). I did not find Knipowitsch's (1892) histological sections of either specimen in the ZIN in 1989, though Wagin (1976) claimed they were there. The lectotype's host actually keys out as *Henricia skorikovi* Djakonov, a supposed White Sea endemic (key of D'yakonov 1968). Madsen (1987) did not include *H. skorikovi* in his revision of *Henricia* of the Norwegian Sea, but noted that it is evidently related to *H. eschrichti* (Müller & Troschel).

Dendrogaster murmanensis Wagin, 1950b

Kluge (1911, 1912) found *Dendrogaster* infesting *Crossaster papposus* (L.) and *Solaster endeca* in the Kola Fjord near the

Murmansk Biological Station. Wagin often gave Kluge (1912) credit for proposing the name *D. murmanensis* for these parasites, as a nomen nudum, but I have found no specific name used in Kluge's reports. While several papers had discussed *D. murmanensis* n. nud. more or less extensively (reviewed by Wagin 1950b), the first one that appears to have met all the requirements for availability was Wagin (1950b) itself.

One of the illustrated specimens included in *D. astericola* by Knipowitsch (1891:fig. 1, 1892:taf. I, fig. 5) actually belongs to *D. murmanensis,* according to Wagin (1950b). I did not find this specimen in Leningrad in 1989. Wagin had access to Kluge's specimens, at least some of which fill a large number of uncatalogued bottles and tubes in the ZIN (Acc. no. 144-1957 in part, remainder unaccessioned; reidentified by me in 1989); in most bottles the cryptic and incomplete labels are dated either between 1911 and 1913 or as 1927 and they occasionally refer to Kluge or the Murmansk Biological Station or one of the host species.

Two lots, one labeled "N6, N7, N3" and consisting of three females taken from *Crossaster* on 3 Jan 1911, the other labeled "N5" and containing one female collected on 7 Jan 1911, claim to correspond to drawings, but it is unclear which drawings are meant. With regard to "N3," for example, specimen #3 of Wagin (1950b) was collected by him in 1947 (see below), not by Kluge in 1911.

Wagin (1976) wrote that the type specimens are in the ZIN and that paratypes are in the Museums of Leningrad and Kazan Universities; however, there were no specimens in 1989 in the LGU collections. The handwritten label of one accessioned tube in the ZIN reads, "Murmanskaya biologich. Stantsiya. Barentsogo Morye Sb. 2. Al. Kluge. 6-1-1927," with the typewritten notation "Tip" [type]; it contains nine females in good condition, some broken female branches, a vial of eggs, and a vial of three torn pieces possibly of a male but without the main body. Unfortunately I had no time to study this lot in detail, but its specimens cannot fairly be regarded as the only syntypes, not having been so designated by Wagin in 1950.

Wagin (1950b) reported nine females of *D. murmanensis* from *Crossaster papposus* collected off SW Sakhalin in 1947 (ZIN 1/23368). Three specimens are more or less whole and the others are torn and fragmented. None could be matched to illustrations, so none is considered suitable to be named as lectotype.

Dendrogaster rimskykorsakowi Wagin, 1950b

This species is based on four females, one from sta. 57 in the northern Sea of Japan, parasitizing *Ctenodiscus crispatus* Retzius, and three from stas. 57 and 95 in the Sea of Okhotsk off Sakhalin, parasitizing *Hippasteria leiopelta* Fisher. A. V. Ivanov collected additional specimens from *C. crispatus* in the northern Sea of Japan and Tatar Strait, but Wagin saw only some of their larvae.

Wagin (1976:93) invalidly tried to restrict the type lot, "Type specimens in ZIN AN SSSR, out of *Ctenodiscus crispatus.*" [my translation]. The female from this host (ZIN 1/23377), now in five pieces and with the middle piece opened and males removed, was illustrated (Wagin 1950b:fig. 5a; tab. I, fig. 7), and I am naming it the lectotype. Specimens from sta. 57 or 95 (ZIN 2/23378) are paralectotypes and consist of a whole female with an opened middle piece and two isolated males. Although there is only one female, two labels in the jar read "57" and "95–96," hence the ambiguity. The latter designation may mean along the cruise track between stas. 95 and 96 (see Appendix). A vial of metanauplii of this species found packaged together with the types of *D. dogieli* (see below) was also labeled "95–96." Another paralectotype female remains in situ in its host *Hippasteria leiopelta* in

the teaching collection at LGU (shelf A-5); Wagin (1950b:tab. I, fig. 11) published a photograph of this specimen.

Dendrogaster dichotoma Wagin, 1950b

This species was based on three females from sta. 78 in the Tatar Strait and apparently from sta. 81 off eastern Sakhalin. The host was *Crossaster papposus* in the second case and probably also in the first (at least the same genus). The labels in the two bottles of *D. dichotoma* at the ZIN have become confused; ZIN 1/23366 contains the original labels for both stas. 78 and 81 as well as a copied label for sta. 81, and ZIN 2/23367 has no original label, only a copied one for sta. 78. I think the copied labels are in the wrong jars. According to Wagin (1950b), his figs. 10 and 11b ought to be based on the two females from sta. 81, but at the ZIN the smaller female is missing, and the specimen upon which his fig. 10 and tab. I, fig. 8 are based (ZIN 2/23367) is in the bottle labeled sta. 78. 1 am naming the latter specimen the lectotype; it is broken into three big pieces and about 10 small ones, and the tip of its middle piece is gone. The other bottle (ZIN 1/23366) contains a whole paralectotype female and a vial of three paralectotype males (another male may be present in the female's middle piece). Wagin (1950b) only mentioned finding males in the female from the Sea of Japan, i.e., from sta. 78.

Besides these specimens, the parasitology collection at LGU holds two slides (N3316, N3322) of paralectotype males of *D. dichotoma,* neither of them being the models for any illustrations. N3316 displays a male in situ within a mantle branch tip of a brooding female.

Dendrogaster arctica Korschelt, 1933

Grygier (1986) named a lectotype and explained why Korschelt (1933) is the valid author of this specific name, based on Fisher's (1930) material from *Albatross* sta. 3252 in the Bering Sea (host: *Leptasterias groenlandica* (Lütken)). Wagin's (1950b) three females collected from *L. groenlandica* in the Anadyr Gulf are therefore not types despite his later claim to authorship (Wagin 1976). The two adult females illustrated by Wagin (1950b:fig. 15a; tab. I, figs. 9, 10), both broken into several pieces, and four males accompanying the female in his fig. 15a, two of them whole and two dissected, are housed at the ZIN (1/23375). The third, juvenile female is missing.

Dendrogaster dogieli Wagin, 1950b

Two females were found in a single specimen of supposed *Pteraster obscurus* Perrier off SE Sakhalin. The multi-rayed host is actually *P. octaster* Verrill (A. V. Smirnov, in litt.; for taxonomy see Smirnov 1982). The extant type material of *D. dogieli* (ZIN 1/23372) consists of both females photographed by Wagin (1950b:tab. II, figs. 9, 10), one lacking the middle piece, the other with its appendages dissected out; neither is in good enough condition to confirm the large, bifid "extra branch" opposite the middle piece. The smaller of the two is illustrated by a drawing (Wagin 1950b:fig. 17a) and it is chosen as the lectotype; the other female is a paralectotype. A paralectotype male, the one illustrated by Wagin (1950b:fig. 18a), is mounted on a slide (N3320) in the parasitology collection at LGU.

Dendrogaster leptasteriae Wagin, 1950b

This species was described on the basis of specimens or fragments infesting *Leptasterias fisheri* Djakonov at stas. 79 and 81 in the Tatar Strait in 1931 and stas. 67 and 83 in the Sea of Okhotsk near Sakhalin in 1947. There are two lots of syntypes of this species at the ZIN. ZIN 1/23370 is from either or both of the 1931 stations (the label bears the following numbers of unknown significance: 3, 25, 41, 56) and consists of over 20 broken fragments from more than

one female, with no middle pieces among them, and also two vials of eggs and a vial containing two males. Males were only reported from sta. 81. ZIN 2/23374 from sta. 83 consists of three females (two of them with dissected middle pieces), a broken-off mantle branch, and a vial of ascothoracid-larvae. None of the females is the one illustrated by Wagin (1950b:fig. 19a; tab. III, fig. 7). It is unclear whether any are the ones he photographed (Wagin 1950b:tab. II; fig. 3, tab. III, fig. 8). Another female syntype from the Sea of Okhotsk (sta. 67 by elimination; probably Wagin's specimen no. 4) remains in situ within its host in the teaching collection at LGU (shelf A-6); this one was photographed (Wagin 1950b:tab. I, fig. 12) and it is named the lectotype.

Dendrogaster iwanowi Wagin, 1950b

This species was spelled *D. ivanovi* in Wagin (1950a), and it could be argued that this spelling has priority. Three females were found within *Leptasterias fisheri* (questionable field identification) in the Tatar Strait. A damaged one was used by Wagin for histological study. The other two comprise ZIN 1/23373. One is the specimen illustrated by Wagin (1950b:fig. 23a; tab. II, fig. 6), and it is named the lectotype. The other, which has had its middle piece dissected, may have been the model for fig. 24 in that paper, and it is named the paralectotype. I did not find the males described by Wagin.

Dendrogaster astropectinis (Yosii, 1931)

This species was originally described as *Myriocladus astropectinis* from *Astropecten scoparius* Valenciennes in shallow water in Japan. The type locality was unspecified but assumed by Wagin (1950b) to have been Misaki. I have been unable to locate any extant types.

Wagin (1950b) assigned to this species 17 whole and and broken females, together with a number of males, found in 13 *Psilaster pectinatus* Fisher at sta. 4 off the Kamchatka Peninsula. The available material from this station (ZIN 1/23383) consists of five more or less complete females and a great number of large and small fragments without middle pieces, as well a vial with two males labeled "26 & 27." One of the semi-intact females probably corresponds to Wagin's (1950b) fig. 27b; I cannot say for sure whether any correspond to that paper's photographs (tab. I, figs. 1–6).

Wagin also deposited two bottles of this species from the Bering Sea in the teaching collection at LGU (shelves A-4 and A-7), and the latter one contains a specimen in situ in its unidentified host. Sta. 4 is technically not in the Bering Sea (see Appendix), but I think it is safe to assume that these two bottles are from the same lot as those in the ZIN.

Wagin (1957) reported additional material from *Psilaster pectinatus* collected by the *Vityaz* in 1950. A bottle (ZIN 2/23384) containing eight females, seven of them whole, and a vial of three males correspond to at least some of this lot.

Dendrogaster elegans Wagin, 1950b

This name was spelled *elegaus* in Wagin (1950a), and it might be argued that this spelling, perhaps corrected for gender to *elegaa,* has priority; there is no internal evidence in that dissertation summary that *elegaus* was a typographical mistake for *elegans.* The type specimens were found in *Leptasterias* (*Hexasterias*) *polaris* (Müller & Troschel) at four sites in the Bering Sea as well as off the east coast of Sakhalin; no lectotype is named here. Some of the syntypes housed at the ZIN are poorly labeled. One specimen from sta. 82 (ZIN 1/23379) is an immature female broken into two pieces. A bottle labeled as being from Bukhta Natal'ya (ZIN 3/23381) has five isolated mantle pieces and many broken fragments (there should be three specimens from this site—Wagin 1950b) with the following additional indi-

cations on the labels: "48" and "48a," which are interpreted, perhaps wrongly, as station numbers in the Appendix, and "170 m." A third bottle (ZIN 2/23380), with no clear locality data, contains two broken-up females, one of which in my opinion may be mistakenly included in *D. elegans* since it appears very distinctive and has a short middle piece. This bottle also contained labels marked: "1932," "93," "129" (or "124"?), "51 1932," and "52 1932." The numbers other than the years do not correspond to station numbers (A. V. Smirnov, pers. comm.).

Wagin (1957) reported additional specimens of *D. elegans* from *Hexasterias polaris* (=*Leptasterias polaris*) collected in the Anadyr Gulf in the Bering Sea. He wrote that he had deposited two specimens in the ZIN, where I found an undetermined number of individuals lacking middle pieces (ZIN 4/23382); supposedly two more specimens were deposited in the Moscow University Museum, but I could not confirm this.

In the teaching collection at LGU, a bottle on shelf B-3 contains an unidentified *Dendrogaster* together with many specimens of the parasitic eulimid gastropod *Asterophilus* sp., infesting a specimen of *Leptasterias polaris* from the Bering Sea, identified by A. V. Ivanov in 1932. The ascothoracidan appears to be *D. elegans* but could be *D. orientalis* (see below).

Dendrogaster orientalis Wagin, 1950b

The description mentioned material from the Bering Sea in 1932 from a host questionably identified as *Leptasterias polaris* and from stas. 67 and 69 off SE Sakhalin in 1947 from *Leptasterias orientalis* Djakonov. An apparently mixed lot at the ZIN (1/23376) seems to include the specimens collected in 1947: a young, complete female, an incomplete female with a dissected middle piece, and three isolated primary branches perhaps belonging to a third female. There is also a vial of larval exuviae and ascothoracid-larvae. The young specimen is from sta. 67 according to the original label, but the others are most likely from sta. 69, judging from the information given by Wagin (1950b:tab. 12). Although there are drawings and photographs of three of the four original specimens in Wagin's description, I could match none of the present specimens to them, so no lectotype is named.

Dendrogaster ramosa Wagin, 1950b

This species is based on two females infesting supposed *Leptasterias fisheri* (field identification) in the Tatar Strait. The large specimen (ZIN 1/23369) and the small one (ZIN 2/23371) both have dissected middle pieces and the former is lacking its reported males. Both specimens were illustrated; the large one (Wagin 1950b:fig. 37; tab. II, fig. 8) is named the lectotype and the small one (Wagin 1950b:fig. 38a; tab. II, fig. 7) is a paralectotype.

Dendrogaster beringensis Wagin, 1957

Seven specimens of this species infesting *Eremicaster tenebriarius* Fisher (i.e., *E. crassus* (Sladen); for taxonomy see Belyaev (1985)) were collected by the *Vityaz* in 1950, apparently at sta. 618 in the Bering Sea. Wagin (1976) reported that he had deposited "all the type specimens" in the ZIN, and kept one together with its host sea-star in the Zoological Museum of Kazan University. Six females are indeed catalogued at the ZIN (1/23385) as *Dendrogaster beringii* (sic), including five in alcohol and a small one mounted whole on a slide. In addition, several uncatalogued slides have recently been transferred from Kazan: 1) female cephalic appendages; 2) a male with one carapace valve separated (illustrated by Wagin 1957:fig. 3b); 3) an antennule from the same male; 4 and 5) nauplii in poor condition. The female which looks most similar to and which may have been the model for Wagin's (1957) fig. 1a is chosen as the lec-

totype; the other female and male specimens are paralectotypes.

Wagin (1976) reported another specimen collected from the same host in 1968 in the Kuril-Kamchatka Trench by the *Vityaz*. However, Wagin must have been mistaken because the *Vityaz* operated in that region in 1966, not 1968 (G. M. Belyaev, pers. comm. via A. V. Smirnov, in litt.). The specimen was not in the ZIN in 1989, and I don't know whether it is in Moscow.

Acknowledgments

I thank T. Wolff (Zoologisk Museum, Copenhagen) for allowing me to examine type specimens there during a visit funded by the American-Scandinavian Foundation and for interceding on my behalf for the initial loan of specimens from the ZIN, and M. Downey (formerly Smithsonian Institution) for helping me to reidentify the host of *Dendrogaster astericola*. My visit to Leningrad was arranged by the National Academy of Sciences Soviet and East European Exchange Program. I thank Ya. I. Starobogatov, I. S. Smirnov, and N. V. Vyshkvartseva (ZIN) and T. A. Ginetsinskaya (LGU) for allowing me to examine Wagin's specimens, and E. L. Markhaseva and especially A. V. Smirnov (ZIN) for providing much background information about them; Dr. Markhaseva provided the Russian abstract. The manuscript was partly prepared while I was a Visiting Foreign Researcher at the Sesoko Marine Science Center, Okinawa, Japan.

Literature Cited

Barel, C. D. N., & P. G. N. Kramers. 1977. A survey of the echinoderm associates of the north-east Atlantic area.—Zoologische Verhandelingen 156: 1–159.

Belyaev, G. M. 1985. Abyssal starfishes of the genera *Eremicaster* and *Abyssaster* (Porcellanasteridae): composition and distribution.—Zoologicheskiy Zhurnal 64:865–876 (in Russian with English summary).

Brattström, H. 1936. *Ulophysema öresundense* n. gen. et sp., eine neue Art der Ordnung Cirripedia Ascothoracica (vorläufige Mitteilung).—Arkiv för Zoologi 28A(23):1–10.

———. 1937. On the genus *Ulophysema* Brattström with description of a new species from East Greenland.—Meddelelser om Grønland 118(7): 1–24.

D'yakonov, A. M. 1968. Sea stars (asteroids) of the USSR seas. Keys to the Fauna of the USSR 34: 1–183 (translation of 1950 Russian text, Israel Program for Scientific Translations, Jerusalem).

Fisher, W. K. 1930. Asteroidea of the North Pacific and adjacent waters. Part 3. Forcipulata (concluded).—United States National Museum Bulletin 76(3):1–356.

Grygier, M. J. 1986. *Dendrogaster* (Crustacea: Ascothoracida) parasitic in Alaskan and eastern Canadian *Leptasterias* (Asteroidea).—Canadian Journal of Zoology 64:1249–1253.

———. 1987. Classification of the Ascothoracida (Crustacea).—Proceedings of the Biological Society of Washington 100:452–458.

Ivanov, A. V. 1933. Über die Erforschungen des Benthos an den Küsten des Ussuri-Landes und der Tatarischen Meeresstrasse im Jahre 1931.—Issledovaniya Morey SSSR 19:93–113 (in Russian with German summary).

Kluge, G. A. 1911. Otchet" zaveduyushchago Murmanskoyu Biologicheskoyu Stantsiyeyu za 1910 g.—Trudy S.-Peterburgskago Obshchestva Yestestvoispytateley 42(I,4):165–183 (in Russian).

———. 1912. Otchet" zaveduyushchago Murmanskoyu Biologicheskoyu Stantiyeyu za 1911 god".—Trudy S.-Peterburgskago Obshchestva Yestestvoispytateley 43(I,4):130–147 (in Russian).

Knipowitsch, N. 1890. *Dendrogaster astericola* nov. g. et sp., novaya forma paraziticheskikh" Cirripedia iz" gruppy Ascothoracida. Predvaritel'noye soobshcheniye.—Vestnik" Yestestvoznaniya 1:353–357 (in Russian).

———. 1891. *Dendrogaster astericola* nov. g. et sp., eine neue Form aus der Gruppe Ascothoracida. Vorläufige Mitteilung.—Biologisches Centralblatt 10:707–711.

———. 1892. Beiträge zur Kenntniss der Gruppe Ascothoracida.—Trudy S.-Peterburgskago Obshchestva Yestestvoispytateley, Otdeleniye Zoologii i Fiziologii 23(2):1–155 (in Russian with German summary).

Korschelt, E. 1933. Über zwei parasitäre Cirripedien, *Chelonibia* und *Dendrogaster*, nebst Angaben über die Beziehungen der Balanomorphen zu ihrer Unterlage.—Zoologische Jahrbücher Abteilung für Systematik, Ökologie und Geographie der Tiere 64:1–39.

Lindberg, G. U. (ed.). 1959. Spisok fauny morskikh vod yuzhnogo Sakhalina i yuzhnukh Kuri-

l'skikh Ostrovov.—Issledovaniya Dal'nevostochnykh Morey SSSR 6:1–39 (in Russian).
Madsen, F. J. 1987. The *Henricia sanguinolenta* complex (Echinodermata, Asteroidea) of the Norwegian Sea and adjacent waters. A re-evaluation, with notes on related species.—Steenstrupia 13(5):201–268.
Smirnov, A. V. 1982. Vidy *Pteraster obscurus* (Perrier, 1891) i *P. octaster* Verrill, 1909 (Asteroidea: Pterasteridae).—Issledovaniya Fauny Morey 29(37):102–113 (in Russian).
Vaghin, V. L. 1946. On males of Dendrogasteridae (Entomostraca, Ascothoracida).—Comptes Rendus (Doklady) de l'Académie des Sciences de l'URSS 52:273–276.
Wagin, V. L. 1948a. O tipakh lichinochnogo razvitiya u Dendrogasteridae (Ascothoracida, Entomostraca).—Doklady Akademii Nauk SSSR 59:387–390 (in Russian).
———. 1948b. O somaticheskoy substitutsii u parazitov.—Doklady Akademii Nauk SSSR 59:387–390 (in Russian).
———. 1950a. Ocherki po evolyutsionnoy morfologii i sistematike paraziticheskikh rakoobraznykh (sem. Dendrogasteridae). Avtoreferat (summary) of Doctor of Biological Sciences dissertation, Leningrad University, Department of Biology and Soil Science, 14 pp. (in Russian).
———. 1950b. O novykh paraziticheskikh rakoobraznykh iz semeystva Dendrogasteridae (otryad Ascothoracida).—Trudy Leningradskogo Obshchestva Yestestvoispytateley 70(4):3–89 (in Russian).
———. 1957. Dendrogasteridae (Entomostraca, Ascothoracida) aus den Asteroidea der Beringsee.—Trudy Leningradskogo Obshchestva Yestestvoispytateley 73(4):58–63 (in Russian with German summary).
———. 1964. On *Parascothorax sinagogoides* (sic) gen. n., sp. n., parasitizing on *Ophiura quadrispina* Glarck (sic) and some remarks on geographical distribution of Ascothoracidae (sic) (Entomostraca).—Trudy Instituta Okeanologii, Akademiya Nauk SSSR 69:271–284 (in Russian with English summary).
———. 1976. Meshkogrudyye Raki. Izdatel'stvo Kazanskogo Universiteta, 141 pp. (Ascothoracida. Kazan University Press) (in Russian).
Yosii, N. 1931. Note on *Myriocladus*.—Journal of the Faculty of Science Imperial University of Tokyo Section IV Zoology 2:337–349.

University of the Ryukyus, Sesoko Marine Science Center, Sesoko, Motobu-cho, Okinawa 905-02, Japan. (Current address) Kyoto University, Seto Marine Biological Laboratory, Shirahama, Nishimuro, Wakayama 649-22, Japan.

Appendix

Full locality data for Dendrogastridae (*Ulophysema* and *Dendrogaster*) found in Soviet waters by A. V. Ivanov and V. L. Wagin and studied by Wagin (1950b, 1957, 1964, 1976). Asterisks (*) indicate localities for which Wagin provided no station number. In these cases station numbers have been tentatively inferred on the basis of other information, such as reported depth or geographical location or indications on specimen labels, and conflicting information is mentioned.

U. pourtalesiae

Wagin & Koltun, C-3 Expedition, sta. 85, 12 Aug 1948, Svyataya Anna Trough, Kara Sea, 78°31′N, 66°44′E, 387 m.

D. murmanensis

Wagin, ZIN Kuril-Sakhalin Expedition, *Toporok,* sta. 15, 7 Aug 1947, Sea of Japan off SW Sakhalin, 47°10.0′N, 141°48.0′E, 165 m, 2.7°C.

D. rimskykorsakowi

Ivanov, Pacific Research Institute of Marine Fisheries and Oceanography (TINRO), *Rossinante,* sta. 57, 31 Jul 1931, N Sea of Japan, 46°15.0–14.8′N, 138°34.2–33.2′E, 627–636 m, 0.11°C.

Ibid., sta. 62, 2 Aug 1931, N Sea of Japan, 47°39.0′N, 139°55.7–59.0′E, 340–410 m, 0.36°C.

Ibid., sta. 74, 6 Aug 1931, N Sea of Japan, 48°14.4′N, 140°51.7′E, 576–592 m, 0.12°C.

Ibid., sta. 82, 10 Aug 1931, Tatar Strait, 50°54.3′N, 141°27.5–25.9′E, 75 m.

Wagin, ZIN Kuril-Sakhalin Expedition, *Toporok,* sta. 57, 12 Sep 1947, Sea of Okhotsk off SE Sakhalin, 46°59.7′N, 143°11.5′E, 52 m, −1.5°C.

Ibid., sta. 95–96, 12 Sep 1947, Sea of Okhotsk off E Sakhalin, 48°47.8–50.5′N, 143°04.1–04.5′E, 33–27 m, 1.6–3.0°C.

D. dichotoma

Ivanov, TINRO, *Rossinante,* sta. 78, 8 Aug 1931, Tatar Strait, 49°14.9–12.7′N, 141°39.8′E, 165–185 m, 1.27°C.

*Wagin, ZIN Kuril-Sakhalin Expedition, *Toporok,* sta. 81, 9 Sep 1947, Sea of Okhotsk off Terpeniya Peninsula, E Sakhalin, 49°01.1′N, 144°37.8′E, 47 m, 2.8°C.

D. arctica

Ivanov, Kamchatka-Bering Strait Expedition, sta. 46, 29 Aug 1932, Anadyr Gulf, Bering Sea, 64°22′N, 179°46′E, 46 m.

D. dogieli

Wagin, ZIN Kuril-Sakhalin Expedition, *Toporok,* sta. 64, 4 Sep 1947, Sea of Okhotsk off SE Sakhalin, 46°48.0′N, 143°48.0′E, 143 m, −0.9°C.

D. leptasteriae

Ivanov, TINRO, *Rossinante,* sta. 79, 9 Aug 1931, Tatar Strait, 50°57.8–56.6′N, 142°02.7–02.4′E, 47 m, 7.26°C.

Ibid., sta. 81, 10 Aug 1931, Tatar Strait, 50°55.4–54.9′N, 141°45.5–42.5′E, 71–73 m, 0.72°C.

Wagin, ZIN Kuril-Sakhalin Expedition, *Toporok,* sta. 67, 5 Sep 1947, Sea of Okhotsk off SE Sakhalin, 47°33.0′N, 143°54.2′E, 144 m, −1.0°C.

Ibid., sta. 83, 9 Sep 1947, Sea of Okhotsk off Terpeniya Peninsula, E Sakhalin, 49°01.0′N, 144°48.5′E, 127 m, −0.7°C.

D. iwanowi

Ivanov, TINRO, *Rossinante,* sta. 85, 10 Aug 1931, Tatar Strait, 50°58.4′–51°00.0′N, 140°44.8–46.0′E, 58–60 m, −0.7°C.

D. astropectinis

Ivanov, Kamchatka-Bering Strait Expedition, sta. 4, 17 Jul 1932, Pacific Ocean off Petropavlovsk, Kamchatka Peninsula, 52°34.7′N, 159°39.1′E, 1500–2000 m.

*Wagin, *Vityaz,* sta. 591, 13 Sep 1950, Bering Sea, 60°52.5′N, 175°22′E, 2160 m or 2200 m (but 2300 m.—Wagin 1957).

D. elegans

Ivanov, Kamchatka-Bering Strait Expedition, sta. 12, 28 Jul 1932, Bering Sea off Mys Navarin, 62°13.0′N, 179°15.0′E, 50 m (but off Mys Povorotnii.—Wagin 1976).

*Ibid., sta. 48, 7 Sep 1932, Bukhta Natal'ya, Bering Sea, 63°34.4′N, 179°49′W, 49 m (but 170 m according to one label; 25 Aug 1932.—Wagin 1950b).

Ibid., sta. 20, 7 Aug 1932, Bering Strait S of Krusenstern Is. (i.e., Little Diomede Is.), 32–40 m.

Ibid., no station mentioned or inferred, 1932, Bering Strait.

Wagin, ZIN Kuril-Sakhalin Expedition, *Toporok,* sta. 82, 9 Sep 1947, Sea of Okhotsk off Terpeniya Peninsula, E Sakhalin, 49°01.0′N, 144°41.5′E, 75 m, 0.8°C.

*Wagin, *Vityaz,* sta. 582, 11 Sep 1950, Bering Sea off Mys Navarin, 62°10.9′N, 179°00.8′E, 42–53 m (but 30–70 m.—Wagin 1957).

D. orientalis

Ivanov, Kamchatka-Bering Strait Expedition, no station mentioned or inferred, 1932, Bukhta Natal'ya, Bering Sea.

Wagin, ZIN Kuril-Sakhalin Expedition, *Toporok,* sta. 67, 5 Sep 1947, Sea of Okhotsk off SE Sakhalin, 47°33.0′N, 143°54.2′E, 144 m, −1.0°C.

Ibid., sta. 69, 5 Sep 1947, Sea of Okhotsk off SE Sakhalin, 47°32.0′N, 143°38.2′E, 128 m, −1.1°C.

D. ramosa

Ivanov, TINRO, *Rossinante,* probably between stas. 81 and 85, 10 Aug 1931, Tatar Strait (sta. 81: 50°55.4–54.9′N, 141°45.4–42.5′E, 71–73 m, 0.72°C; sta 85: 50°58.4′–51°00.0′N, 140°44.8–46.0′E, 58–60 m, −0.7°C).

D. beringensis

Wagin, *Vityaz,* sta. 618, 25 Sep 1950, SW Bering Sea, 57°18.5′N, 168°50′E, 3940 m.

*G. M. Belyaev, *Vityaz,* sta. 5637 or possibly 5603, Kuril-Kamchatka Trench (sta. 5637: 9 Sep 1966, 44°29′N, 149°06′E, 3015–2665 m; sta. 5603: 15 Jul 1966, 46°22′N, 153°03′E, 3175–3250 m) (but 2590 m in 1968.—Wagin 1976; *Vityaz* operated in this area in 1966, not 1968.—Belyaev, pers. comm. via A. V. Smirnov, in litt.).

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 751–757

REDIAGNOSIS AND REVISION OF SOME NANNASTACIDAE (CRUSTACEA: CUMACEA)

Les Watling

Abstract.—The genera *Cumella* and *Nannastacus* have become large and diffuse, and are defined by only a few characters. New diagnoses are given for these genera, as well as for the related *Schizotrema,* and the genus *Cumella* is divided into four subgenera. In addition, *Schizocuma* is reinstated, and the new genera *Scherocumella* and *Elassocumella* are created. It is suggested that the genera with separated siphons originated independently, *Schizocuma* in deep water and *Schizotrema* in shallow water.

The taxonomy of the Cumacea has remained quite stable during its history. Few of the earlier genera have been revised or changed in concept, although several genera have been added. As a consequence, some genera have become quite large and their definitions diffuse. In the Nannastacidae, there are 17+ genera, the number varying depending on which of several proposed new genera one is willing to accept. Most of these genera contain only a few species, but three (*Campylaspis, Cumella,* and *Nannastacus*) have 30 or more.

Three genera, *Cumella, Nannastacus,* and *Schizotrema,* have been defined historically by only a few characters, e.g., general shape of the carapace, condition of the eye, and condition of the branchial siphon and pseudorostral lobes. Often, one or two characters have been given much more weight than others. For example, the possession of a split eyelobe and medially united branchial siphon was reason enough to assign a species to the genus *Nannastacus.* As noted by Zimmer (1941) the genus soon came to consist of two groups—those with a long pseudorostrum and long uropod peduncles, and those with a short pseudorostrum and short uropod peduncles. There is a clear need to define more narrowly these nannastacid genera so that each is homogeneous and is defined by a larger suite of characters.

In this paper I emend the diagnoses of the genera *Cumella, Nannastacus,* and *Schizotrema,* divide *Cumella* into several subgenera, reinstate the genus *Schizocuma,* and propose two new genera, one for an odd species previously assigned to *Cumella,* and another for a group of species removed from the genus *Nannastacus.*

Cumella Sars, 1865

Styloptocuma Bacescu & Muradian, 1974.—Jones, 1984.

Type species.—*Cumella pygmaea* Sars, 1865.

Diagnosis (emended).—Carapace anteroventral corner acute to slightly rounded, not strongly projecting; ocular lobe single, middorsal; siphons united medially, occasionally slightly separated; pseudorostral lobes of varying length, usually slightly to strongly upturned, meeting in front of eyelobe; antenna 1 peduncle article 2 with or without process, subequal to or longer than article 3; female maxilliped 3, pereopods 1 and 2 with exopods; male maxilliped 3 and pereopods 1–4 with exopods; uropod peduncle usually as long as or longer than pleonite 6; uropod exopod basal article short, not submerged in peduncle, exopod much longer than its terminal seta.

Subgenus *Cumella* Sars, 1865

Type species.—*Cumella pygmaea* Sars, 1865.

Diagnosis.—Eyelobe with or without lenses, narrow, short, not reaching end of pseudorostral lobes.

Additional species.—*Cumella* (*Cumella*) *aculeata* Jones, 1984; *C.* (*C.*) *africana* Bacescu, 1977; *C.* (*C.*) *agglutinanta* Bacescu, 1971; *C.* (*C.*) *argentinae* Jones, 1984; *C.* (*C.*) *arguta* Gamô, 1962; *C.* (*C.*) *australis* Calman, 1907; *C.* (*C.*) *cana* Hale, 1945; *C.* (*C.*) *carinata* (Hansen, 1887); *C.* (*C.*) *compacta* Jones, 1984; *C.* (*C.*) *coralicola* Bacescu, 1971; *C.* (*C.*) *decipiens* Jones, 1984; *C.* (*C.*) *dentata* Lomakina, 1952; *C.* (*C.*) *garrityi* Bacescu & Muradian, 1977; *C.* (*C.*) *gomoiui* Bacescu & Muradian, 1977; *C.* (*C.*) *gurwitchi* Lomakina, 1952; *C.* (*C.*) *hastata* Fage, 1945; *C.* (*C.*) *hirsuta* (Hansen, 1895), new combination; *C.* (*C.*) *hispida* Calman, 1911; *C.* (*C.*) *laevis* Calman, 1911; *C.* (*C.*) *lima* Hale, 1936; *C.* (*C.*) *meredithi* Bacescu, 1971; *C.* (*C.*) *meridionalis* Jones, 1984; *C.* (*C.*) *michaelseni* Zimmer, 1914; *C.* (*C.*) *munroi* Hale, 1945; *C.* (*C.*) *pilosa* Bacescu, 1971; *C.* (*C.*) *polita* Jones, 1984; *C.* (*C.*) *quadrispinosa* Gamô, 1965; *C.* (*C.*) *rigida* Gamô, 1963; *C.* (*C.*) *sadoensis* Gamô, 1967; *C.* (*C.*) *scabera* Gamô, 1962; *C.* (*C.*) *similis* Fage, 1945; *C.* (*C.*) *spicata* Jones, 1984; *C.* (*C.*) *tarda* Hansen, 1920; *C.* (*C.*) *tripunctata* Bacescu, 1971; *C.* (*C.*) *vicina* Zimmer, 1944; *C.* (*C.*) *vulgaris* Hart, 1930.

Remarks.—Included in this list is *C.* (*C.*) *hirsuta,* originally assigned to *Nannastacus* by Hansen (1895). While it has a slightly enlarged eyelobe, and appears to have the lenses partitioned into two groups, the uropods are most characteristic of the genus *Cumella.*

Subgenus *Cumewingia* Bacescu, 1971

Type species.—*Cumella caribbeana* Bacescu, 1971.

Diagnosis.—Eyelobe with lenses, narrow, short, not reaching end of pseudorostrum, in male augmented by lenses on pseudorostrum.

Additional species.—*Cumella* (*Cumewingia*) *alveata* Gamô, 1964a; *C.* (*C.*) *clavicauda* Calman, 1911; *C.* (*C.*) *forficula* Calman, 1911; *C.* (*C.*) *forficuloides* Bacescu & Muradian, 1975; *C.* (*C.*) *glaberata* Gamô, 1962; *C.* (*C.*) *indosinica* Zimmer, 1952; *C.* (*C.*) *leptopus* Calman, 1911; *C.* (*C.*) *limicola* Sars, 1879; *C.* (*C.*) *limicoloides* Bacescu & Muradian, 1975; *C.* (*C.*) *schieckei* Bacescu & Muradian, 1975; *C.* (*C.*) *serrata* Calman, 1911; *C.* (*C.*) *siamensis* Zimmer, 1952; *C.* (*C.*) *turgidula* Hale, 1945.

Subgenus *Styloptocuma*
Bacescu & Muradian, 1974

Type species.—*Styloptocuma antipai* Bacescu & Muradian, 1974.

Diagnosis (emended).—Eyelobe without lenses, narrow, generally elongate, reaching to end of or beyond pseudorostral lobes.

Additional species.—*Cumella* (*Styloptocuma*) *acuminata* Jones, 1984; *C.* (*S.*) *angustata* Jones, 1984; *C.* (*S.*) *bishopi* Jones, 1984; *C.* (*S.*) *concinna* Jones, 1984; *C.* (*S.*) *cristata* Jones, 1984; *C.* (*S.*) *dayae* Jones, 1984; *C.* (*S.*) *echinata* Jones, 1984; *C.* (*S.*) *egregia* Hansen, 1920; *C.* (*S.*) *erecta* Jones, 1984; *C.* (*S.*) *exstans* Jones, 1984; *C.* (*S.*) *formosa* Jones, 1984; *C.* (*S.*) *gracillima* Hansen, 1920; *C.* (*S.*) *longisipho* Jones, 1984; *C.* (*S.*) *subducta* Jones, 1984.

Remarks.—While the elongate eyelobe strongly typifies this group, they are all also unusually long and slender, both in body and appendages. Jones (1984) described several other species which were also long and slender but are not included in this subgenus because of their short eyelobes. If one hypothesizes that the eyelobe is a synapomorphy characterizing a deep-sea phylogenetic lineage, then the other long and slender species have independently invaded this environment.

Cyclaspocumella, new subgenus

Type species.—*Cumella cyclaspoides* Zimmer, 1914.

Diagnosis.—Eyelobe with or without lenses, broad, reaching end of pseudorostral lobes.

Etymology.—From *Cyclaspis,* a cumacean genus, + *cumella,* referring to the *Cyclaspis*-like shape of the carapace.

Additional species.—*Cumella* (*Cyclaspocumella*) *gibba* Zimmer, 1914.

Remarks.—The two species listed for this subgenus were both described from Shark Bay, Western Australia, one, *C.* (*C.*) *cyclaspoides,* from a single female, and the other, *C.* (*C.*) *gibba,* from a single male. It is possible, in fact, that they are the same species, but further material will be needed to make this determination. The membership of *C.* (*C.*) *gibba* in *Cumella* is questionable since it possesses exopods only on maxilliped 3 and pereopods 1–3, with the last being slightly reduced.

Elassocumella, new genus

Type species.—*Cumella micruropus* Zimmer, 1943.

Diagnosis.—Carapace anteroventral corner broadly rounded; ocular lobe single, mid-dorsal; siphons united medially; pseudorostral lobes of moderate length, not upturned, meeting in front of eyelobe; antenna 1 peduncle article 2 without process, subequal to article 3; exopods absent from maxilliped 3 and pereopods in female; uropod peduncle shorter than pleonite 6; uropod exopod basal article not submerged in peduncle, exopod longer than its terminal seta; abdomen shorter than cephalothorax; male unknown.

Etymology.—From Greek, *elasso,* diminished, + *cumella*; feminine.

Additional species.—No others.

Remarks.—Zimmer (1943, 1980) recognized that the lack of exopods made this species unique within the genus *Cumella* but attached no particular significance to the shortness of the uropod peduncles or the abdominal somites. However, in its possession of this combination of features, it has few in common with the other *Cumella* species, and by its inclusion serves only to dilute the concept of that genus.

Nannastacus Bate, 1865

Type species.—*Cuma unguiculata* Bate, 1859.

Diagnosis (emended).—Carapace anteroventral corner large, acute, strongly projecting; ocular lobe divided, eyes when present located dorsolaterally; branchial siphon united medially; pseudorostral lobes short, directed slightly upward; antenna 1 peduncle article 2 usually with process, subequal in length to peduncle article 3; female maxilliped 3 and pereopods 1 and 2 with exopods, occasionally missing on maxilliped 3; male maxilliped 3 and pereopods 1–4 with exopods; uropod peduncle in male shorter than or equal in length to pleonite 6; uropod exopod basal article very short, often submerged in peduncle, exopod shorter than its terminal seta.

Additional species.—*Nannastacus angulifera* Lomakina, 1967; *N. agnatus* Calman, 1911; *N. asper* Hale, 1945; *N. brevicaudatus* Calman, 1905; *N. erinaceus* Zimmer, 1913; *N. euxinicus* Bacescu, 1951; *N. gibbosus* Calman, 1911; *N. goniatus* Gamô, 1962; *N. hanseni* Calman, 1905; *N. inconstans* Hale, 1945; *N. inflatus* Hale, 1945; *N. johnstoni* Hale, 1945; *N. minor* Calman, 1911; *N. mystacinus* Zimmer, 1921; *N. nudus* Gamô, 1962; *N. nyctagineus* Gamô, 1962; *N. pardus* Calman, 1905; *N. parvulus* Bacescu & Muradian, 1975; *N. pectinatus* Gamô, 1962; *N. pruinosus* Gamô, 1962; *N. reptans* Calman, 1911; *N. sauteri* Zimmer, 1921; *N. spinosus* Gamô, 1962; *N. spinulosus* Gamô, 1962; *N. stebbingi* Calman, 1904; *N. subinflatus* Hale, 1945; *N. suhmii* Sars, 1887; *N. tardus* Calman, 1911; *N. turcicus* Baces-

cu, 1982; *N. umbellulifer* Gamô, 1963; *N. zimmeri* Calman, 1911.

Remarks.—Zimmer (1941) noted that the genus consisted of two groups of species—those with a short pseudorostrum and short uropod peduncles, and those with a long pseudorostrum and long uropod peduncles. The first group consists of species most like the type species of the genus, *N. unguiculatus.* The latter group possesses additional characters of its own and has been removed into a separate genus, *Scherocumella* (described below). Fage (1945) subdivided *Nannastacus* into three groups: 1) those which now make up the new genus, *Scherocumella*; 2) those where the uropod exopod is remarkably short and the endopod is fringed with setae; and 3) those where the uropod exopod is relatively long and the endopod is serrate and has several, often long, setae. The second group is distinguished also by the absence of exopods from the third maxillipeds in several species and from both the third maxillipeds and pereopods 1 and 2 in two species. The latter two, *N. reptans* Calman, 1911 and *N. tardus* Calman, 1911, were assigned to a new genus, *Paranannastacus* by Stebbing (1912). Zimmer (1921), Hale (1945), and Fage (1945) did not accept this genus, arguing that the variable loss of exopods is not significant in *Nannastacus.* As more species are found and other characters are considered, it may be that *Paranannastacus* should be reinstated and that a new genus be considered for the species missing exopods only from the third maxillipeds. The evolution of this genus seems to be in the direction of loss of exopods; the natatory function of the exopod (that is, where the basis is enlarged to accommodate the musculature necessary for powerful swimming strokes) is already lost in *N. agnatus* and *N. minor,* for example.

Scherocumella, new genus

Type species.—*Nannastacus longirostris* Sars, 1879.

Diagnosis.—Carapace anteroventral corner in female acute or subacute, not projecting; ocular lobe divided, eyes dorsolateral; siphons united medially; pseudorostral lobes elongate, united in front of head; antenna 1 peduncle article 2 shorter than or equal to 3, with or without process; female maxilliped 3 and pereopods 1 and 2 with exopods; male maxilliped 3 and pereopods 1–4 with exopods; uropod peduncle longer than pleonite 6; uropod exopod basal article normal, exopod usually at least as long as its terminal seta.

Etymology.—*schero,* Greek, in a line, successive, + *cumella,* referring to the apparent derivation of these forms from the genus *Cumella*; feminine.

Additional species.—*Scherocumella brachydactyla* (Calman, 1905), new combination; *S. clavata* (Hale, 1945), new combination; *S. gurneyi* (Calman, 1927), new combination (more completely described in Bacescu & Muradian, 1975); *S. japonica* (Gamô, 1962), new combination; *S. leptura* (Calman, 1911), new combination; *S. nasuta* (Zimmer, 1914), new combination; *S. nichollsi* (Hale, 1949), new combination; *S. pilgrimi* (Jones, 1963), new combination; *S. sheardi* (Hale, 1945), new combination; *S. stephenseni* (Fage, 1945), new combination; *S. vieta* (Hale, 1949), new combination.

Remarks.—Of the above listed species, *S. nichollsi, S. vieta, S. clavata, S. stephenseni,* and *S. pilgrimi* seem to be transitional in form between *Nannastacus* and *Scherocumella. S. nichollsi* shows the characters of the new genus most strongly, whereas the others, which are known only from the male, lack the elongate pseudorostral lobes but have very long uropod peduncles. The latter species may ultimately have to be removed to another genus. The name chosen for this genus refers to its apparent derivation from *Cumella* rather than *Nannastacus,* the genus from which all the species have been removed. This is based on the strong similarity of carapace shape and uropod structure between *Cumella* and *Scherocumella.* The form of the uropod in *Nannastacus,*

with its very short peduncle and highly reduced exopod, would seem to be more apomorphic, and perhaps derived independently from a *Cumella*-like form.

Schizotrema Calman, 1911

Type species.—*Schizotrema depressum* Calman, 1911.

Diagnosis (emended).—Carapace anteroventral corner acute, projecting; ocular lobe divided, eyes located dorsolaterally; branchial siphons separate, located laterally; pseudorostral lobes located dorsolaterally; antenna 1 peduncle article 2 usually shorter than 3, with process; female maxilliped 3 and pereopods 1 and 2 with exopods; male maxilliped 3 and pereopods 1–4 with exopods; uropod peduncle shorter than or equal in length to pleonite 6; uropod exopod basal article minute, nearly submerged in peduncle, exopod nearly as long as or longer than its terminal seta.

Additional species.—*Schizotrema aculeatum* Hale, 1936; *S. atlanticum* Bacescu & Muradian, 1972; *S. bidens* Fage, 1945; *S. bifrons* Calman, 1911; *S. depressum* Calman, 1911; *S. leopardinum* Hale, 1949; *S. macrodactylus* Fage, 1945; *S. resimum* Hale, 1949; *S. sakaii* Gamô, 1964b; *S. sordidum* Calman, 1911.

Remarks.—The members of this genus, until the discovery of the most recent species, were known only from very shallow waters in the Indo-Pacific. *S. atlanticum* is unique in being found at greater than 200 m depth.

Schizocuma Bacescu, 1972

Type species.—*Schizocuma vemae* Bacescu, 1972.

Diagnosis (emended).—Carapace anteroventral corner rounded or subacute; ocular lobe incompletely subdivided, located medially; branchial siphons separated, located medially to dorsolaterally; pseudorostral lobes separated; antenna 1 peduncle article 2 without process, subequal in length to article 3; maxilliped 3 and pereopods 1 and 2 with exopods in female; maxilliped 3 and pereopods 1–4 with exopods in male; uropod peduncle much longer than pleonite 6; uropod exopod basal article normal, exopod shorter than its terminal seta.

Additional species.—*Schizocuma calmani* (Stebbing, 1912), new combination; *S. divisa* (Jones, 1984), new combination; *S. molossa* (Zimmer, 1907), new combination; *S. spinoculata* (Jones, 1984), new combination; *S. spinosa* (Jones, 1984), new combination.

Remarks.—This genus was distinguished from *Cumella* by Bacescu (1972) chiefly on the basis of its separated siphons, but also using as criteria the slenderness and elongation of the body and appendages. Jones (1984) argued that since there seemed to be a gradation in body and appendage form with no obvious grouping of species in the genus *Cumella,* he could not accept *Schizocuma* as a valid genus, and that *S. vemae, S. calmani,* and *S. molossa* should remain in *Cumella.* On the other hand, he recognized that *S. calmani* did not belong in the genus *Schizotrema.* In my opinion, the combination of separated siphons, dorsolaterally located pseudorostral lobes, and single eyelobe (although in some species it may be indented) serves to unite this rather disparate deep-dwelling group of species. From a phylogenetic perspective, it is likely that this apomorphic genus evolved from *Cumella* in deep waters, whereas *Schizotrema,* which also has separated siphons, evolved from *Nannastacus* in shallow waters.

Acknowledgments

This study was conducted during the tenure of a Smithsonian Senior Postdoctoral Fellowship. The support of the Smithsonian Institution is greatly appreciated. I would also like to thank Dr. T. E. Bowman for critically reading an earlier version of this paper and for helping me to understand the broader concepts of taxonomy. Comments made by the reviewers helped to stimulate

my thinking with regard to the importance of the eyelobe in these genera. This is Darling Marine Center Contribution No. 240.

Literature Cited

Bacescu, M. 1951. *Nannastacus euxinicus* n. sp., cumaceu nou gasit în apele Marii Negre.—Comunicarile Academiei Republicii Populaire Rômane 1:185–192.

———. 1971. New Cumacea from the littoral waters of Florida (Caribbean Sea).—Travaux du Muséum d'Histoire Naturelle Grigore Antipa 11: 5–23.

———. 1972. *Archaeocuma* and *Schizocuma,* new genera of Cumacea from the American tropical waters.—Revue Roumaine de Biologie, Série de Zoologie 17:241–250.

———. 1982. Contributions à la connaissance des Cumacés de la mer de Marmara et d'Égée (IIe Eubea).—Travaux du Muséum d'Histoire Naturelle Grigore Antipa 24:44–54.

———, & Z. Muradian. 1972. Nouvelles espèces de Nannastacidae (Crustacés, Cumacés) dans les eaux sahariennes de l'Atlantique.—Revue de Travaux Institut Pêches maritimes 36:255–269.

———, & ———. 1974. *Campylaspenis, Stylopto-cuma, Atlantocuma,* new genera of Cumacea from the deep waters of the Atlantic.—Revue Roumaine de Biologie, Série de Zoologie 19:71–79.

———, & ———. 1975. New Cumacea from the Red Sea.—Travaux du Muséum d'Histoire Naturelle Grigore Antipa 16:35–69.

———, & ———. 1977. Species of the genus *Cumella* (Cumacea, Nannastacidae) from the western tropical Atlantic.—Travaux du Muséum d'Histoire Naturelle Grigore Antipa 18:89–101.

Bate, C. S. 1859. On some British Diastylidae.—Annals and Magazine of Natural History, Series 3 3:273–274.

———. 1865. Carcinological gleanings, No. 1.—Annals and Magazine of Natural History, including Zoology, Botany, and Geology, Series 3 15:81–88.

Calman, W. T. 1904. Report on the Cumacea collected by Professor Herdman, at Ceylon, in 1902.—Report to the Government of Ceylon on the pearl oyster fisheries of the Gulf of Manaar, Supplementary Report 12:159–180.

———. 1905. The Cumacca of the Siboga Expedition.—Siboga-Expeditie 36:1–23.

———. 1907. Crustacea. 2. Cumacea.—National Antarctic Expedition. Natural History 2:1–6.

———. 1911. On new or rare Crustacea of the Order Cumacea from the collection of the Copenhagen Museum. Part II. The Families Nannastacidae and Diastylida.—Transactions of the Zoological Society of London 18:341–399.

———. 1927. Zoological results of the Cambridge expedition to the Suez Canal, 1924. Report on the Phyllocarida, Cumacea, and Stomatopoda.—Transactions of the Zoological Society 22: 399–401.

Fage, L. 1945. Les Cumacés du plancton nocturne des côtes d'Annam.—Archives de Zoologie expérimentale et générale 84:165–224.

Gamô, S. 1962. On the cumacean Crustacea from Tanabe Bay, Kii Peninsula.—Publications of the Seto Marne Biological Laboratory 10:154–210.

———. 1963. On the cumacean Crustacea obtained from Amami-Oshima Island, southern Japan.—Science Reports of the Yokohama National University 2:29–60.

———. 1964a. A new cumacean Crustacea, *Cumella alveata* sp. nov., from Sagami Bay.—Bulletin of the Biogeographical Society of Japan 23:23–28.

———. 1964b. On three new species of Cumacea from the southern Sea of Japan.—Crustaceana 7:241–253.

———. 1965. On three new species of Cumacea, Crustacea, from Akkeshi Bay.—Publications from the Akkeshi Marine Biological Station 14: 1–21.

———. 1967. Studies on the Cumacea (Crustacea, Malacostraca) of Japan. Part II.—Publications of the Seto Marine Biological Laboratory 15: 245–274.

Hale, H. M. 1936. Cumacea from a South Australian reef.—Records of the South Australian Museum 5:404–438.

———. 1945. Australian Cumacea. No. 9. The Family Nannastacidae.—Records of the South Australian Muscum 8:145–218.

———. 1949. Australian Cumacea. No. 16. The Family Nannastacidae.—Records of the South Australian Museum 9:225–245.

Hansen, H. J. 1887. Malacostraca marina Groenlandiae occidentalis: oversigt over det vestlige Grønlands fauna af malakostrake havskrebsdyr.—Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn for Aarene (Kjøbenhavn) 9:195–223.

———. 1895. Isopoden, Cumaceen und Stomatopoden der Plankton-Expedition.—Ergebnisse der in dem Atlantischen Ocean von Mitte Juli bis Anfang November 1889 ausgeführten Plankton-Expedition der Humboldt-Stiftung 2 (G,c): 1–105.

———. 1920. Crustacea Malacostraca, IV: The Order Cumacea.—Danish Ingolf Expedition, Copenhagen 3(6):1–74.

Hart, J. F. L. 1930. Some Cumacea of the Vancouver Island region.—Contributions to Canadian Biology and Fisheries, n.s., 6:25–40.

Jones, N. S. 1963. The marine fauna of New Zealand: crustaceans of the Order Cumacea.—New Zealand Oceanographic Institute Memoir No. 23: 1–81.

———. 1984. The Family Nannastacidae (Crustacea: Cumacea) from the deep Atlantic.—Bulletin of the British Museum (Natural History), Zoology Series 46:207–289.

Lomakina, N. B. 1952. Novye interesnye v zoogeograficheskom otnoshenii nakhodki kumovykh rakov v dal'nevostochnykh moryakh. [New zoogeographically interesting findings of Cumacea in far eastern seas.]—Zoologicheskii Zhurnal 30:244–248. (In Russian)

———. 1967. Novye vedyi kumovye (Crustacea, Cumacea) iz sborov Sovetckoye Antarcticheskoi ekspedichii (1956–1958) u yogo-vostochnoye Australii i v severnoye chasti Indiiskogo okeana. [New species of Cumacea collected by the Soviet Antarctic expedition at south-eastern Australia and in the north of the Indian Ocean.]—Trudy Zoologicheskogo Institute, Leningrad 43:99–108.

Sars, G. O. 1865. Om den aberrante krebsdyrgruppe Cumacea og den nordiske Arter.—Forhandlinger i Videnskabs-Selskabet i Christiania (1864): 128–208.

———. 1879. Middlehavets Cumaceer.—Archiv for Mathematik og Naturvidenskab 3:461–512, 4: 1–144.

———. 1887. Report on the Cumacea collected by H.M.S. Challenger during the years 1873–1876.—Report on the Scientific Results of the Voyage of the H.M.S. Challenger During the Years 1873–1876 under the Command of George S. Nares and Frank Tourle Thomson 19(55):1–78.

Stebbing, T. R. R. 1912. The Sympoda (Part VI of S. A. Crustacea, for the marine investigations in South Africa).—Annals of the South African Museum 10:129–176.

Zimmer, C. 1907. Neue Cumaceen von der Deutschen und der Schwedischen Südpolar-expedition aus den Familien der Cumiden, Vaunthompsoniiden, Nannastaciden und Lampropiden.—Zoologischer Anzeiger 31:367–374.

———. 1913. Die Cumacean der Deutschen Südpolar-expedition 1901–1903.—Deutsche Südpolar-Expedition (1901–1903) 14:437–491.

———. 1914. Cumacea.—Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwestaustralischen Forschungsreise 1905 5:175–195.

———. 1921. Cumacea. Results of Dr. E. Mjöbergs Swedish scientific expeditions to Australia, 1910–1913.—Kunglica Svenska Vetenskapsakademiens Handlingar 61:1–13.

———. 1941. Cumacea.—Dr. H. G. Bronn's Klassen und Ordnungen des Tierrichs 5(1)4:1–222.

———. 1943. Über neue und weniger bekannte Cumaceen.—Zoologischer Anzeiger 141:148–167.

———. 1944. Cumaceen des tropischen Westatlantiks.—Zoologischer Anzeiger 144:121–137.

———. 1952. Indochinesische Cumaceen.—Mitteilungen aus dem Zoologischen Museum in Berlin 28:5–35.

———. (ed. by T. Bowman & L. Watling). 1980. Cumaceans of the American Atlantic boreal coast region (Crustacea: Peracarida).—Smithsonian Contributions to Zoology 302:1–29.

Darling Marine Center, University of Maine, Walpole, Maine 04573, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 758–763

SYNISOMA WETZERAE, A NEW SPECIES AND THE FIRST RECORD OF *SYNISOMA* FROM THE NEW WORLD (CRUSTACEA: ISOPODA: VALVIFERA: IDOTEIDAE)

Bernard Ormsby

Abstract.—The first species of *Synisoma* (Isopoda: Valvifera: Idoteidae), *S. wetzerae,* to be reported from the New World is described from Catalina Island, California.

The idoteid isopod fauna of the northeast Pacific is largely summarized in Menzies (1950), Menzies & Miller (1972), Brusca & Wallerstein (1977, 1979a, 1979b), and Brusca (1983, 1984). The present study reports on a new species of the genus *Synisoma* collected by A. Chess from Catalina Island, California. This represents the first reported record of *Synisoma* from the New World.

The terminology used in this paper follows that of previous idoteid isopod literature (Menzies 1950, Brusca 1983). The following abbreviations are used: USNM, National Museum of Natural History; SDNHM, San Diego Natural History Museum; LACM, Los Angeles County Natural History Museum.

Systematics Paleontology

Order Isopoda Latreille, 1817
Suborder Valvifera Sars, 1882
Family Idoteidae Fabricius, 1798
Subfamily Idoteinae Dana, 1852
Genus *Synisoma* Collinge, 1917
Synisoma wetzerae, new species
Fig. 1

Types.—Holotype: female, LACM 87-294.1; 6 (2 ♂, 4 ♀). Paratypes LACM 87-294.2; 8 (4 ♂, 4 ♀). Paratypes to SDNHM (2128–2135); 6 (3 ♂, 3 ♀). Paratypes to USNM (243565).

Type locality.—All specimens are from one locality: California, Santa Catalina Island (33°25.4′N, 118°30.8′W); "Isthmus Reef"; found on the brown algae *Sargassum palmeri,* and *Cystoseira neglecta*; depth 13 m; 10 Mar 1987; collected by A. Chess (National Marine Fisheries Service, Tubiron, California).

Diagnosis.—Pleotelson longer than wide; all pleomeres fused, without lateral incisions or any trace of sutures dorsally or ventrally; coxal plates not visible in dorsal aspect; cephalon with distinct dorsal tubercle; smooth (without sculpturing), pereon without dorsal keel; antennal flagellum multiarticulate; maxillipedal palp 4-articulate (suture between second and third article obscure); maxillipedal endite with one coupling hook and distal spines and plumose setae; male appendix masculina very long, nearly twice length of pleopod rami.

Description.—Body smooth and elongate, 9–10 times longer than wide (gravid females noticeably wider, but not noticeable longer); length of specimens in type series 3.4–10.6 mm; lightly pigmented, pale brown in alcohol (Fig. 1).

Cephalon: With a distinct, slightly elongate mid-dorsal tubercle; eyes dark, round, on lateral edge of cephalon. Antennule with 3-articulate peduncle and 1-articulate flagellum; flagellum with simple setae and 7 aesthetascs. Antenna with 4-articulate peduncle and 8- to 10-articulate flagellum, the distalmost one or two articles being minute; all flagellar articles with simple setae. Right mandible with 4-toothed incisor; weakly developed lacinia mobilis with one large incisor and a 5 to 6 serrate setal row; and a

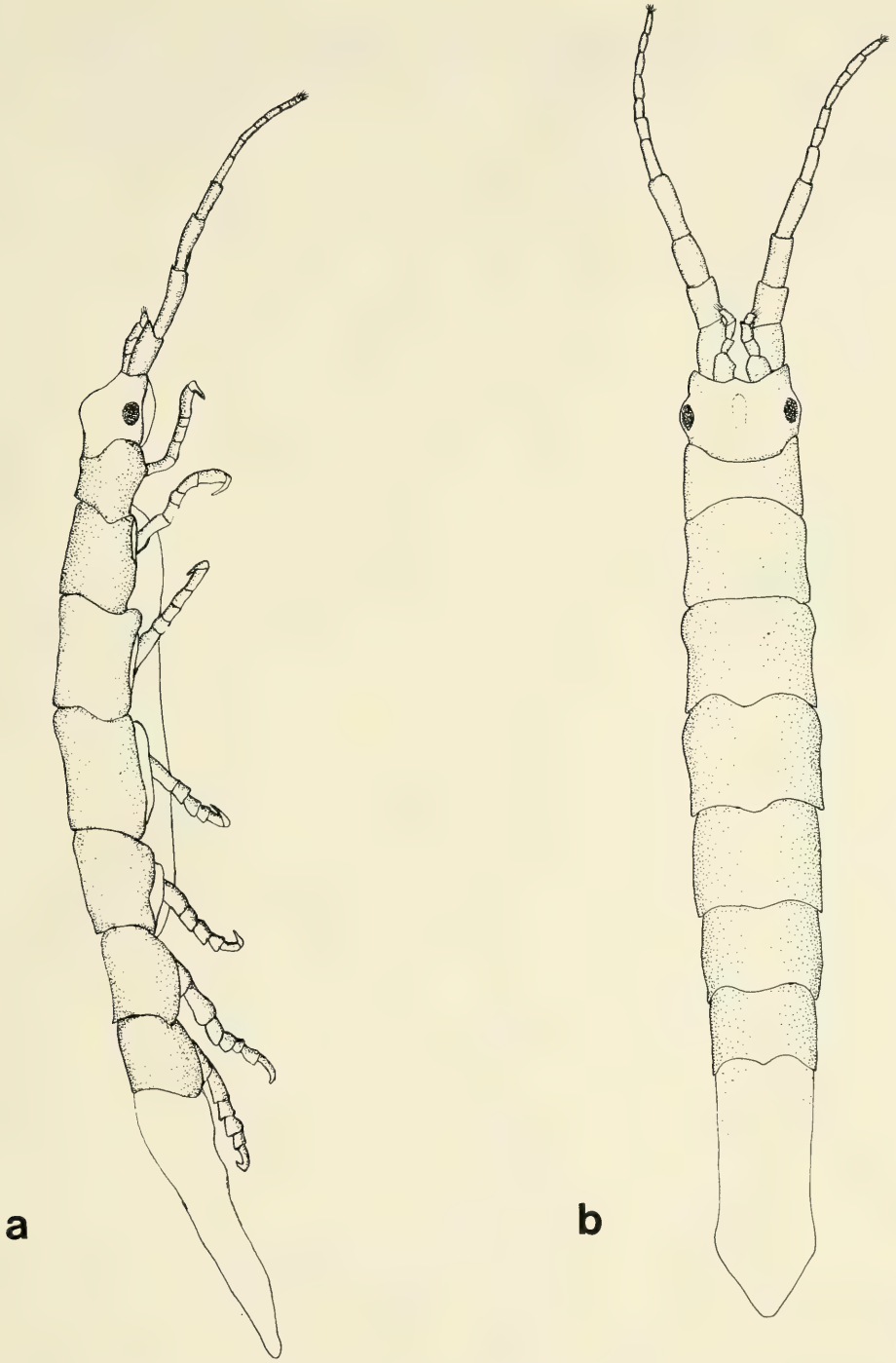


Fig. 1. *Synisoma wetzerae,* new species (holotype, ♀, LACM (Cat. No. 87-294.1)); a, Rt lateral exterior view (coxal plates are not visible per this view on pereonites 6, 7); b, Dorsal exterior view.

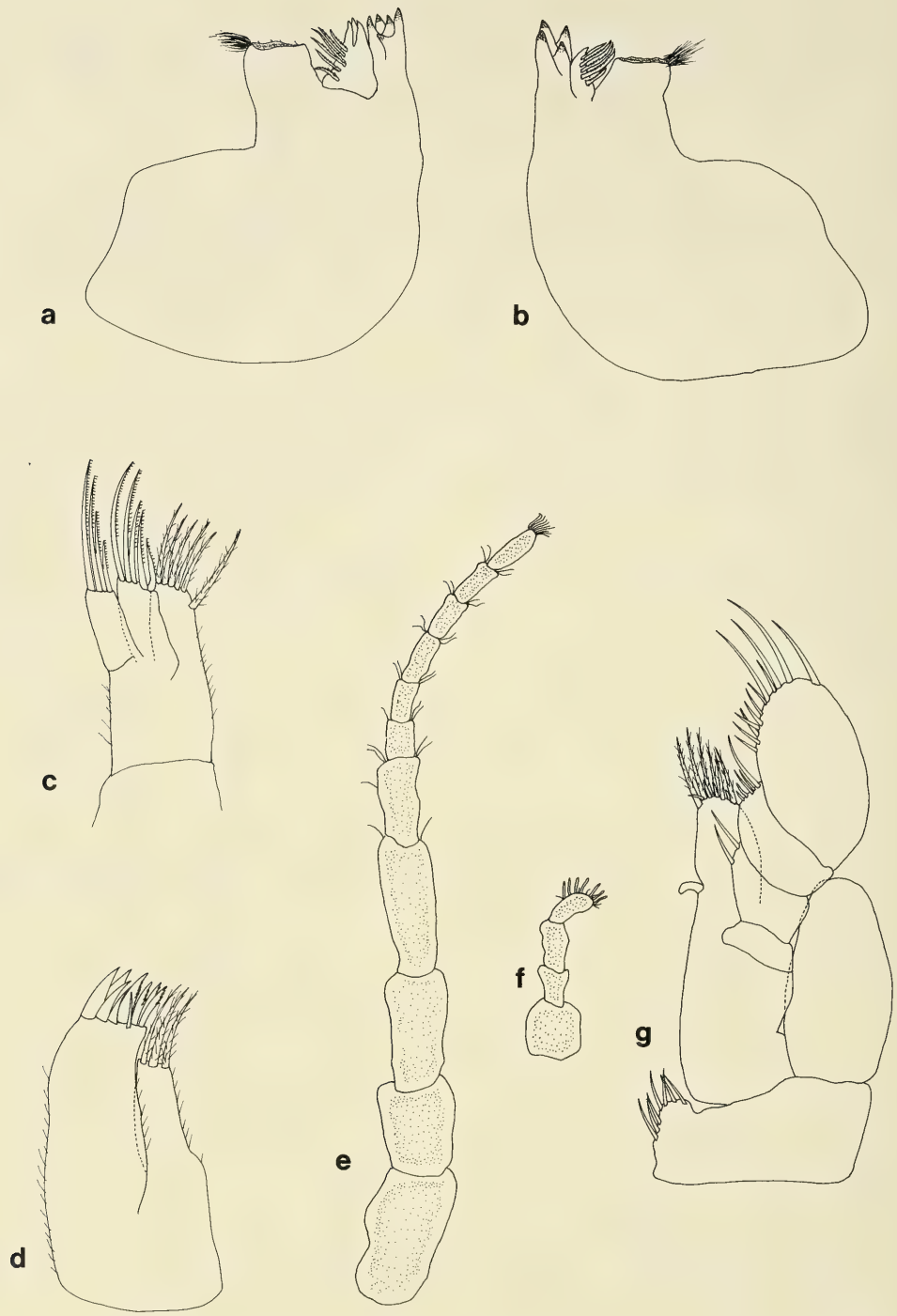


Fig. 2. Mouthparts of *Synisoma wetzerae*, new species (holotype, ♀, Rt side); a, Lt mandible; b, Rt mandible; c, Maxillule; d, Maxilla; e, Antenna; f, Antennule; g, Maxilliped.

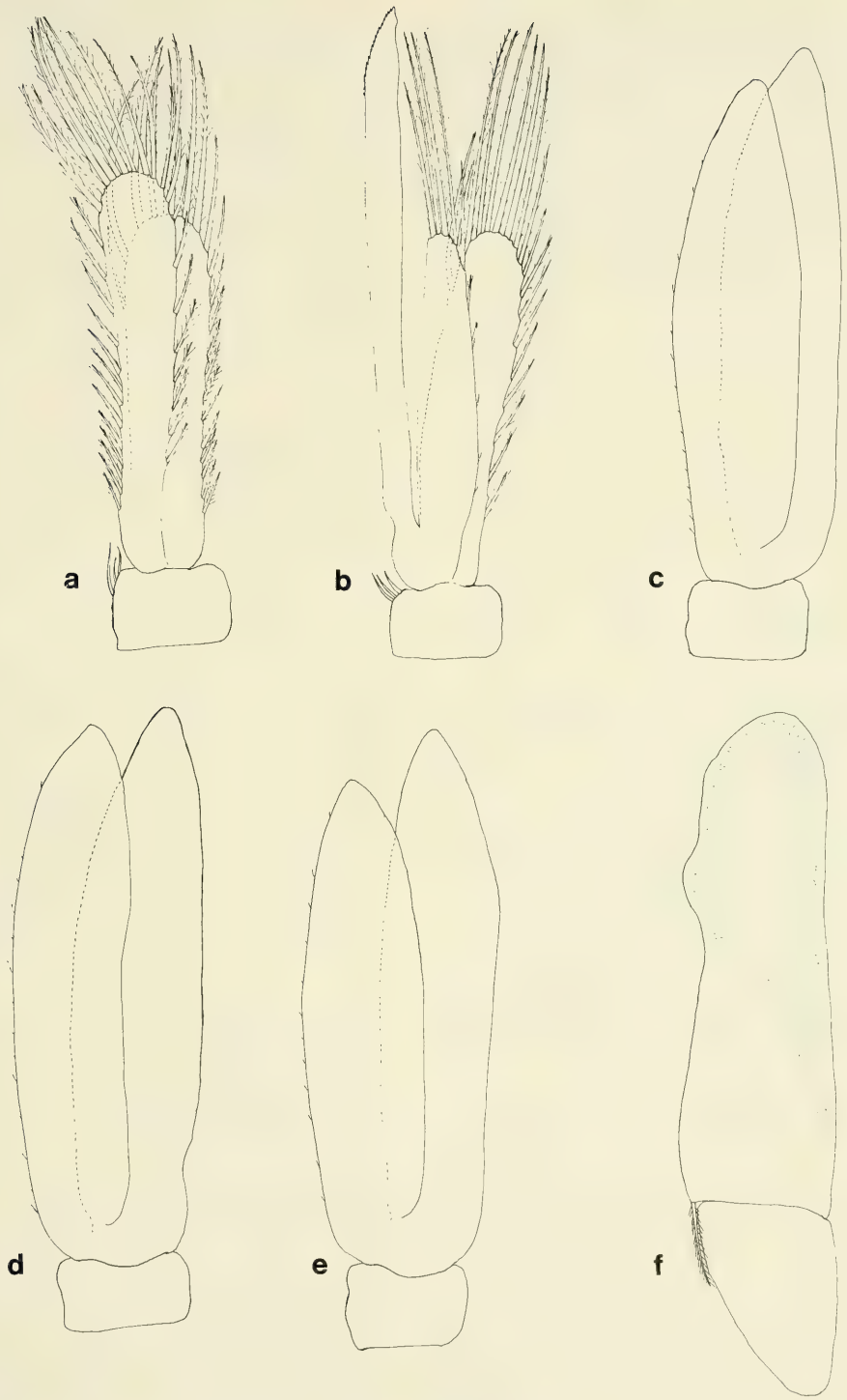


Fig. 3. *Synisoma wetzerae*, new species (holotype, ♀ (except b–c), Rt side); a, First pleopod; b, Second pleopod (paratype, ♂, LACM (Cat. No. 87-294.2)); c–e, Pleopods 3–5; f, Uropod.

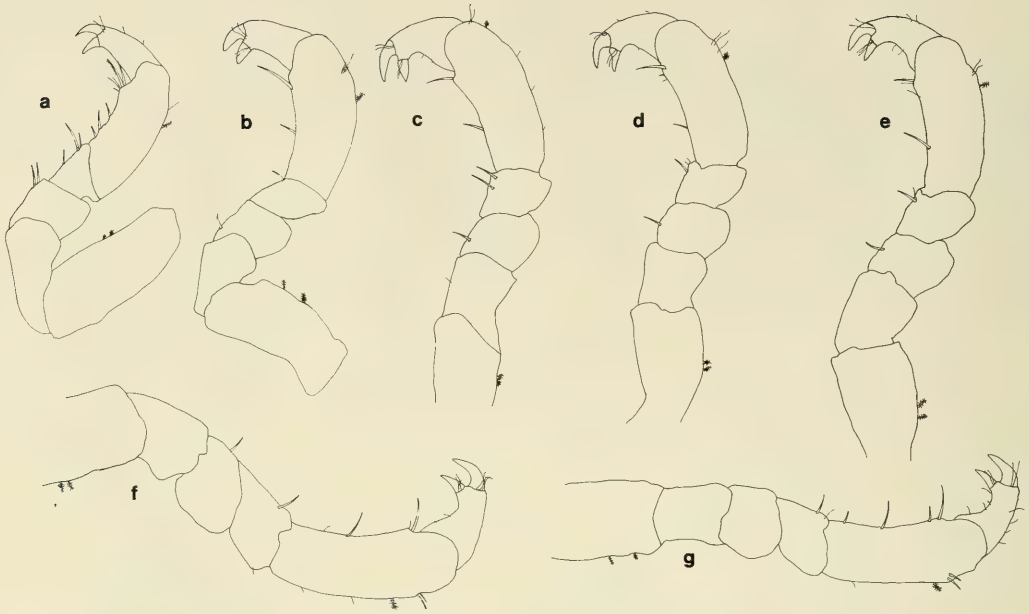


Fig. 4. *Synisoma wetzerae*, new species (holotype, Rt side); a–g, Pereopods 1–7.

large molar process. Left mandible with 5-toothed incisor; complex lacinia mobilis with 3 large incisors and 5 to 6 serrate setal row; and a less pronounced molar process. Maxillule innerlobe with 3 distal circumplumose setae; outerlobe with 4 large and one small, stout simple setae and 4 stout serrate spines. Maxilla innerlobe with circumplumose setae; medial and outer lobe with 4 to 5 comb setae each. Maxilliped palp 4-articulate, articulation between second and third articles obscure; endite with one coupling hook, 4 apical spines, and 4 to 6 long circumplumose setae (Fig. 2).

Pleon: All pleonal segments fused; no visible sutures. Pleon margins slightly concave for three quarters of its length, but flaring somewhat distally and with subacute posterior margin. Pleotelson 2 to 3 times longer than wide. Pleopods 1–2 with plumose marginal setae on rami and simple setae on inner margins of peduncles. Pleopods 3–5 larger than 1–2, without plumose marginal setae but with a few simple setae along the inner margin of the endopod. Appendix masculinum of male is very large, blade-shaped, and distally serrate. Uropodal peduncle with one large, stout, plumose, distomedial seta (Fig. 3).

Pereon: Pereonites II–VII longer than pereonite I. Coxal plates small and compact, not visible in dorsal aspect. Pereopods I–VII ambulatory, terminating in a biungulate dactyl with simple setae. All pereopods with small palmate setae on basis and on distal superior margin of propodus (Fig. 4).

Etymology.—*Synisoma wetzerae* is named for Regina Wetzer, in appreciation of her many years of support and assistance, her interest in isopod systematics, and her long-standing friendship.

Discussion.—There are currently 10 nominate species of *Synisoma*: *S. acuminatum* (Leach, 1815), *S. lancifer* (Miers, 1883), *S. capito* (Rathke, 1837), *S. appendiculata* (Risso, 1816), *S. carinata* (Lucas, 1849), *S. spinosa* Amar, 1957, *S. bellonae* Daguerre de Hureaux, 1968, *S. mediterranea* Rezig, 1989 and *S. nadejda* Rezig, 1989 found in the old world; *S. pacificum* Nunomura, 1974 occurs in Japanese waters.

Synisoma wetzerae is most closely similar

in overall body form to *S. acuminatum* and *S. pacificum*. *S. wetzerae* can be easily distinguished by the shape of the pleotelson, the coxal plates being hidden from view in the dorsal aspect, the large cephalic middorsal process, the lack of a dorsal carina or keel on the pereonites and pleon, and complete fusion of the pleomeres. There is some confusion regarding the number of partialy fused pleomeres on the pleotelson of the genus as a whole. Species in the genus have 0, 1, or 3 partially fused pleomers. None are currently known to have separate pleomers.

The genus *Synisoma* is restricted to the Northern Hemisphere. Two species are now known from the Pacific: *S. wetzerae* from the north-eastern Pacific, and *S. pacificum* from the north-western Pacific. Brusca (1984), in his biogeographic analysis of the Idoteidae, postulated that the genera *Synisoma* and *Colidotea* are sister groups and vicariant descendants of a once widespread circum-global northern Tethyian track fauna. Brusca indicated that the absence of *Synisoma* from the modern New World fauna was anomalous and could only be explained by extinction. The discovery of a living species of *Synisoma* in the eastern Pacific thus corroborates Brusca's historical inferences regarding this genus.

Acknowledgments

I am grateful to R. C. Brusca for bringing this new species to my attention and for providing information and guidance used in the preparation of this paper. Thanks to J. W. Martin and T. Stebbins of the Los Angeles County Museum of Natural History for technical assistance, review of the manuscript and laboratory space. Thanks also to T. Chess who originally collected these specimens and sent them to R. C. Brusca for examination. I also thank W. Hamner for providing the encouragement for this study.

Literature Cited

Brusca, R. C. 1983. Two new idoteid isopods from Baja California and the Gulf of California (Mexico) and an analysis of the evolutionary history of the genus *Colidotea* (Crustacea: Isopoda: Idoteidae).—Transactions of the San Diego Society of Natural History 20(4):69–79.

———. 1984. Phylogeny, evolution and biogeography of the marine isopod subfamily Idoteinae (Crustacea: Isopoda: Idoteidae).—Transactions of the San Diego Society of Natural History 20(7): 99–133.

———, & B. R. Wallerstein. 1977. The marine isopod crustaceans of the Gulf of California. I. Family Idoteidae.—American Museum Novitates 2634:1–17.

———, & ———. 1979a. The marine isopod crustaceans of the Gulf of California. II. Idoteidae. New genus, new species, new records and comments on the morphology, taxonomy and evolution within the family.—Proceedings of the Biological Society of Washington 92:253–271.

———, & ———. 1979b. Zoogeographic patterns of idoteid isopods in the northeast Pacific, with a review of shallow-water zoogeography for the region.—Bulletin of the Biological Society of Washington 3:67–105.

Collinge, W. E. 1917. A revision of the British Idoteidae, a family of marine isopods.—Transactions of the Royal Society of Edinburgh, Vol. LI, Part III (No. 23):721–760.

Menzies, R. J. 1950. The taxonomy, ecology and distribution of northern California isopods of the genus *Idothea* with the description of a new species.—Wasmann Journal of Biology 8(2):155–195.

———, & M. A. Miller. 1972. Systematics and zoogeography of the genus *Synidotea* (Crustacea: Isopoda) with an account of Californian species.—Smithsonian Contributions to Zoology 102:1–33.

Naylor E. 1972. British marine isopods. Academic Press, London, 86 pp. [Synopses of the British Fauna, n. ser., No. 3, The Linnean Soc. London.]

Rezig, M. 1989. Les Idoteidae du genre *Synisoma* Collinge (Isopoda Valvifera) du littoral tunisien.—Revue Faculte Science Tunis (D) 4:29–80.

Natural History Museum of Los Angeles County, Department of Crustacea, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 764–792

REVISION OF THE AMERICAN CALLIANASSIDAE (CRUSTACEA: DECAPODA: THALASSINIDEA)

Raymond B. Manning and Darryl L. Felder

Abstract.—Two families, one new, and seven subfamilies, six new, are recognized for taxa previously assigned to the Callianassidae. The new family, Ctenochelidae, includes those taxa having a cardiac prominence on the carapace and an appendix masculina on male Plp2 and lacking a dorsal plate on the uropodal exopod. Three new ctenochelid subfamilies are recognized: Ctenochelinae, for the genera *Ctenocheles, Gourretia, Paracalliax,* and the new genus *Dawsonius,* all of which lack a dorsal oval on the carapace and have a slender propodus and dactylus on Mxp3, Plp2–5 similar in size and shape, and finger-like appendices internae on Plp3–5; Anacalliinae, containing only *Anacalliax,* which has a dorsal oval, a slender propodus and dactylus on Mxp3, and Plp1–2 different from Plp3–5, with Plp3–5 having stubby appendices internae; and Callianopsinae, containing only *Callianopsis,* which has a dorsal oval, an ovate propodus and dactylus on Mxp3, and Plp2–5 similar, with finger-like appendices internae. The family Callianassidae is restricted to those genera lacking both a cardiac prominence on the carapace and an appendix masculina on male Plp2, and which have a dorsal plate on the uropodal exopod. The nominate subfamily includes six genera with a dorsal oval on the carapace, a slender propodus and dactylus on Mxp3, and stubby appendices internae on Plp3–5: *Callianassa, Trypaea,* and *Calliapagurops,* a genus of uncertain position, and three new genera recognized here for American species: *Biffarius, Neotrypaea,* and *Notiax.* Three new callianassid subfamilies are recognized: Callichirinae, comprising five genera, *Callichirus, Corallianassa, Glypturus, Lepidophthalmus,* and *Neocallichirus,* which have a dorsal oval on the carapace, an ovate propodus and slender dactylus on Mxp3, and stubby appendices internae on Plp3–5; Eucalliinae, for *Calliax* and the new genus *Eucalliax,* which lack a dorsal oval on the carapace and have an ovate propodus and dactylus on Mxp3 and finger-like appendices internae on Plp3–5; and Cheraminae, for *Cheramus* and *Scallasis,* which have a dorsal oval, a slender propodus and dactylus on Mxp3, and slender Plp3–5, each with a finger-like appendix interna.

This study began as an attempt to construct a framework for future studies on American callianassids by examining potential generic characters and defining new genera for a disparate variety of species now placed in *Callianassa* Leach, 1814. Despite the superficial similarity of appearance of callianassids in general, our studies of callianassids in the laboratory and in the field convinced us that this genus comprises a heterogeneous assemblage of taxa that did not reflect major differences in morphology and biology in its members (see also discussions in Borradaile 1903, De Man 1928b, Gurney 1944, Biffar 1971a, De Saint Laurent 1973, De Saint Laurent & LeLoeuff 1979, and De Saint Laurent 1979; for overview see Ferrari 1981). Our analysis of characters of American species led us to conclude that the genus *Callianassa* was a

composite of numerous genera and that the family Callianassidae as currently defined (see De Saint Laurent 1973) also was a composite.

This report includes a redefinition at the family level of all callianassid genera as well as a revision at the generic level of almost all American callianassids. Not included is *Callianassa setimanus* (DeKay, 1844) (=*Callianassa atlantica* Rathbun, 1926), which we are placing in a new genus (Manning & Felder, in preparation; in the key to American genera of Callianassidae given below it would key out to *Neotrypaea,* differing from it in lacking a distally projecting lobe on the merus of Mxp3). Also omitted is *Callianassa minima* Rathbun, 1901, in which the scaphognathite lacks the setose margin characteristic of the callianassids and is ornamented instead by a single seta, characteristic of the axiids. We believe that *C. minima* should be placed in the family Thomassiniidae De Saint Laurent, 1979.

One genus included in the Callianassidae by Borradaile (1903), *Calliactites* Borradaile, 1903, was placed in the family Callianideidae De Man, 1928 as a synonym of *Callianidea* H. Milne Edwards, 1837 by De Saint Laurent (1973). It is not considered further here.

Otherwise, all nominal Recent genera formerly placed in the Callianassidae are diagnosed here and all nominal American species formerly placed in *Callianassa* are assigned to different genera. We have made no attempt to accommodate all extralimital species into the genera recognized here.

Figures are provided for most taxa, and all characters that we consider to be diagnostic are figured; some important diagnostic features are indicated by arrows. In addition to figures showing diagnostic characters of individual genera, we have included comparative figures of important morphological features, including the anterior region of the carapace (Fig. 1), some characters of the carapace (Fig. 2), Mxp3 (Fig. 3), major chelipeds (Fig. 4), abdomens and tail fans (Fig. 5), and appendices internae (Fig. 6). The overall appearance of representatives of four genera is shown in Fig. 7. We provide keys to American subfamilies and genera even though we are aware that several other new genera remain to be characterized for species now undescribed so that a key at this stage is necessarily incomplete. The keys do serve to summarize characters that we consider important at both familial and generic levels.

Abbreviations include: A1 (antennule or first antenna), A2 (antenna or second antenna), cl (postorbital carapace length), fm (fathoms), m (meters), Mxp3 (third maxilliped), P (pereopod), Plp (pleopod), and USNM (National Museum of Natural History).

We use the following terminology in describing the shape of the cornea, Mxp3, and appendices internae on the pleopods, each of which appears to be constant at the generic level:

Cornea.—Embedded and indistinct, as in *Callianassa* (Figs. 1, 8b); dorsal and disk-shaped or flattened, as in *Neocallichirus* (Fig. 1); subglobular, as in *Corallianassa* (Fig. 2); and lacking pigment or absent, as in *Paracalliax* (Fig. 1).

Mxp3 (Fig. 3).—Pediform, as in *Anacalliax* and *Callianassa*: ischium-merus length more than three times merus width; subpediform, as in *Neocallichirus*: ischium-merus length about two times merus width; operculiform, as in *Callichirus* and *Trypaea*: ischium-merus length less than two times merus width. The propodus and dactylus are both ovate in Eucalliinae and Callianopsinae, both slender in the Callianassinae, Cheraminae, Ctenochelinae, and the Anacalliinae, and the propodus is ovate and the dactylus is slender in the Callichirinae. Gurney's (1944) comments on the potential value of the shape of the Mxp3 propodus as an important character were prophetic.

Appendices internae (Fig. 6).—Finger-like or digitiform, as in *Cheramus*; stubby and projecting from margin of endopod, as in

Callianassa; stubby and embedded in margin of endopod, as in *Callichirus*.

In characterizing the carapace (Fig. 2), we refer to the presence or absence of a cardiac prominence, a dorsal oval, a rostral spine, and a rostral carina. When present, the cardiac prominence is most evident in lateral view on the posterior midline of the carapace, where it appears as a tubercle or low keel, as in *Anacalliax* and *Ctenocheles*. The dorsal oval, when present, as in *Anacalliax, Cheramus,* and *Glypturus,* is confined to the anterior two-thirds to three-fourths of the carapace and is defined by a distinct groove or furrow that delimits an oval, anterior portion of the carapace in both dorsal and lateral views; posteriorly the dorsal oval is delimited by a distinctly indented cervical groove. In taxa lacking a dorsal oval, the cervical groove is suture-like, not indented mid-dorsally. All taxa shown in Fig. 2 have a rostral spine, a median projection of the carapace that extends at least to the cornea and may over-reach the eye. Relatively few genera have a rostral carina, but it is distinct in *Anacalliax* (Fig. 17) and *Ctenocheles* (Fig. 2).

Major characters of callianassid and ctenochelid subfamilies are summarized in Table 1.

Key to Callianassid-like Families

Male Plp2 with appendix masculina. Uropodal exopod longitudinally carinate dorsally, lacking dorsal plate. Carapace usually with cardiac prominence ..... Ctenochelidae

Male Plp2 without appendix masculina. Uropodal exopod not longitudinally carinate dorsally, with dorsal plate. Carapace without cardiac prominence ..... Callianassidae

Family Callianassidae Dana, 1852

Callianassidae Dana, 1852:12, 14.

Diagnosis.—Carapace lacking cardiac prominence. Antennal scale, if present, rudimentary. Male Plp2, if present, lacking appendix masculina. Plp1–2 smaller than and different from Plp3–5, latter with stubby appendices internae. Uropodal exopod not carinate dorsally, with dorsal plate, lateral notch or incision usually absent.

Type genus.—*Callianassa* Leach, 1814.

Included genera.—*Biffarius,* new genus, *Callianassa, Calliapagurops, Neotrypaea,* new genus, *Notiax,* new genus, and *Trypaea* in the nominate subfamily; *Callichirus, Corallianassa, Glypturus, Lepidophthalmus,* and *Neocallichirus* in the new subfamily Callichirinae; *Cheramus* and *Scallasis* in the new subfamily Cheraminae; and *Calliax* and *Eucalliax,* new genus, in the new subfamily Eucalliinae.

Key to American Subfamilies and Genera of Callianassidae

1. Mxp3 dactylus ovate. Carapace lacking dorsal oval. (Plp3–5 with finger-like appendices internae) ... . Eucalliinae (single American genus *Eucalliax*)
– Mxp3 dactylus slender, digitiform. Carapace with dorsal oval 2
2. Plp3-5 with finger-like appendices internae ..... Cheraminae (single American genus *Cheramus*)
– Plp3-5 with stubby appendices internae 3
3. Mxp 3 propodus oval, as broad as long, width more than twice dactylus width (Callichirinae) 4
– Mxp3 propodus slender, much longer than broad, width at most slightly greater than that of dactylus (Callianassinae) 8
4. Abdomen with strong pattern formed by symmetrical grooves and integumental glands on somites 3–5. Uropodal endopod strap-shaped ..... *Callichirus*
– Abdomen lacking strong pattern formed by symmetrical grooves and integumental glands on somites 3–

Table 1.—Major characters of the callianassid and ctenochelid subfamilies; + = present, − = absent.

	Callianassidae				Ctenochelidae		
	Callia-nassinae	Calli-chirinae	Chera-minae	Eucal-liinae	Cteno-chelinae	Anacal-linae	Callia-nopsinae
Number of genera	6	5	2	2	4	1	1
Cardiac prominence	−	−	−	−	+	+	+
Appendix masculina	−	−	−	−	+	+	+
Dorsal plate on uropodal exopod	+	+	+	+	−	−	−
Strong antennal scale	−	−	−	−	+	+	+
Dorsal oval	+	+	+	−	−	+	+
Plp2–5 similar	−	−	−	−	+	−	+
Mxp3 propodus and dactylus ovate	−	−	−	+	−	−	+
Mxp3 propodus ovate, dactylus slender	−	+	−	−	−	−	−
Mxp3 propodus and dactylus slender	+	−	+	−	+	+	−
Plp3–5 appendices internae finger-like	−	−	+	+	+	−	+

5. Uropodal endopod not strap-shaped 5
5. Mxp3 with exopod. A1 peduncle longer and stouter than A2 peduncle. (Carapace with distinct, upraised rostral spine) .. *Lepidophthalmus*
- Mxp3 without exopod. A1 peduncle neither longer nor stouter than A2 peduncle 6
6. Plp3–5 with appendices internae embedded in margin of endopod. Rostral spine, if present, small, falling short of cornea. (Cornea dorsal, disk-shaped, subterminal; front sometimes weakly trispinous) .... *Neocallichirus*
- Plp3–5 with appendices internae projecting from margin of endopod. Distinct, upturned rostral spine present, extending to cornea. (Front strongly trispinous) 7
7. Carpus and palm of cheliped with 3 dorsal spines. Cornea disk-shaped, dorsal, narrower than stalk ... *Glypturus*
- Carpus and palm of chelipeds unarmed. Cornea subglobular, appearing distal, as wide as stalk .... *Corallianassa*
8. Plp3–5 with appendices internae embedded in margin of endopod. Mxp3 merus projecting beyond articulation with carpus .... *Neotrypaea,* new genus
- Plp3–5 with appendices internae projecting from margin of endopod. Mxp3 merus not projecting beyond articulation with carpus 9
9. Carapace with rostral spine. Male with both Plp1 and Plp2 present .. .. *Notiax,* new genus
- Carapace without rostral spine. Male with Plp2 vestigial or absent .... *Biffarius,* new genus

Subfamily Callianassinae Dana, 1852

Diagnosis.—Carapace with dorsal oval. Mxp3 pediform, sub-pediform, or operculiform, propodus and dactylus slender. Plp3–5 with stubby appendices internae.

Type genus.—*Callianassa* Leach, 1814.

Callianassa Leach, 1814
Figs. 1, 3, 4, 6, 8

Callianassa Leach, 1814:400. Type species *Cancer Astacus subterraneus* Montagu, 1808, by monotypy. Gender feminine.

Diagnosis.—Carapace lacking rostral spine. Cornea embedded, subterminal, indistinct. A1 peduncle not longer and stouter than A2 peduncle. Mxp3 without exopod, ischium-merus pediform; merus not projecting beyond articulation with carpus. Chelipeds unequal, major with meral hook. Plp1 uniramous in both sexes; Plp2 bira-

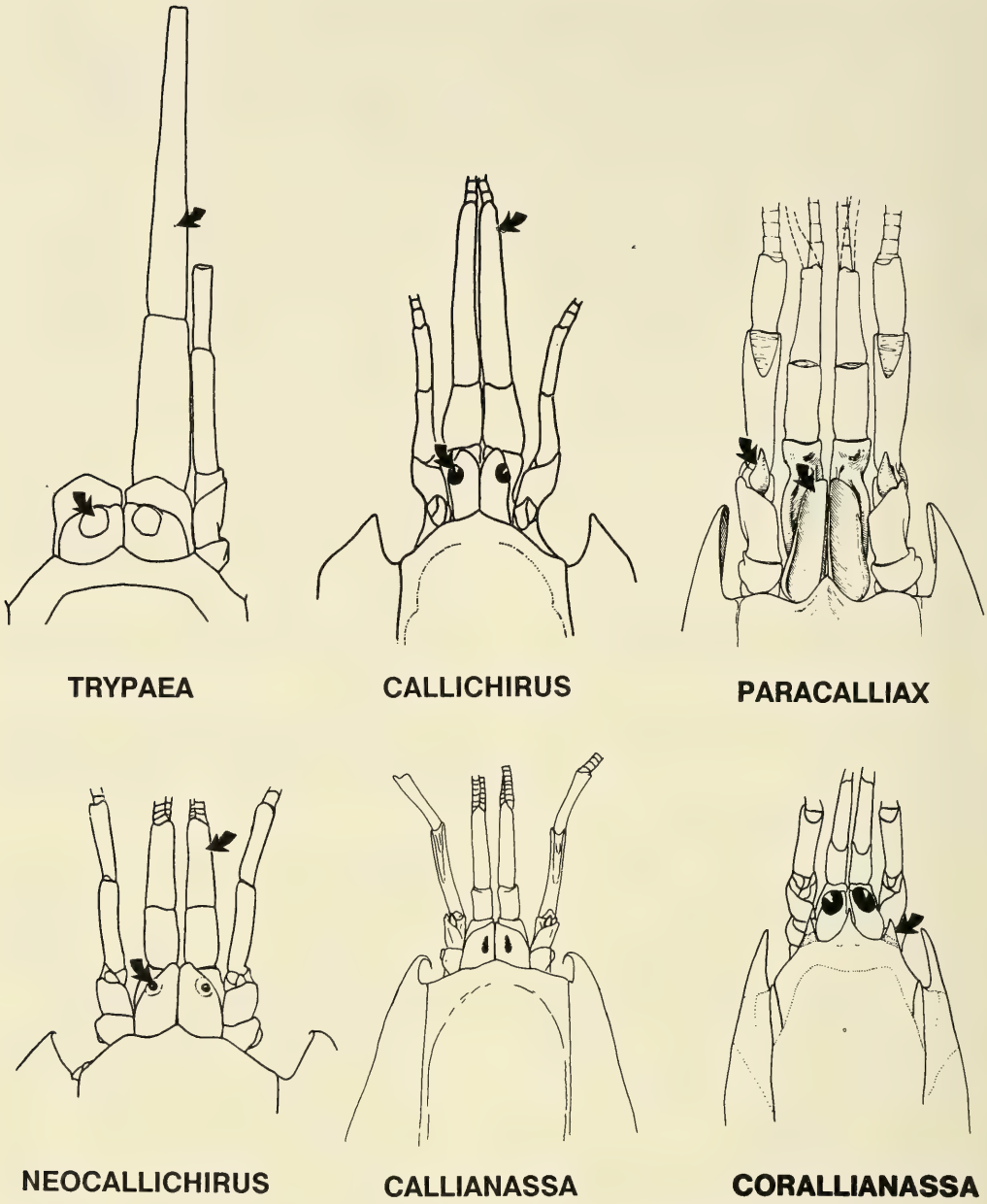


Fig. 1. Anterior region of carapace showing diagnostic features in some callianassid and ctenochelid genera. *Callianassa: C. subterranea* (Montagu), male, cl 12.0 mm, Scotland, USNM 252395; *Callichirus: C. major* (Say) (from Manning & Felder 1986: fig. 1a); *Corallianassa: C. xutha* Manning (from Manning 1988: fig. 3b); *Neocallichirus: N. horneri* Sakai (from Sakai 1988: fig. 7a); *Paracalliax: P. bollorei* De Saint Laurent (from De Saint Laurent & Le Loeuff 1979: fig. 26b); *Trypaea: T. australiensis* Dana (from Poore & Griffin 1979: fig. 2a).

mous in female, vestigial or absent in male; Plp3–5 foliaceous in both sexes, with stubby, projecting appendices internae (Fig. 6).

American species.—None.

Remarks.—*Callianassa* is the only genus in the subfamily with a slender, pediform third maxilliped.

One species, *Callianassa subterranea*

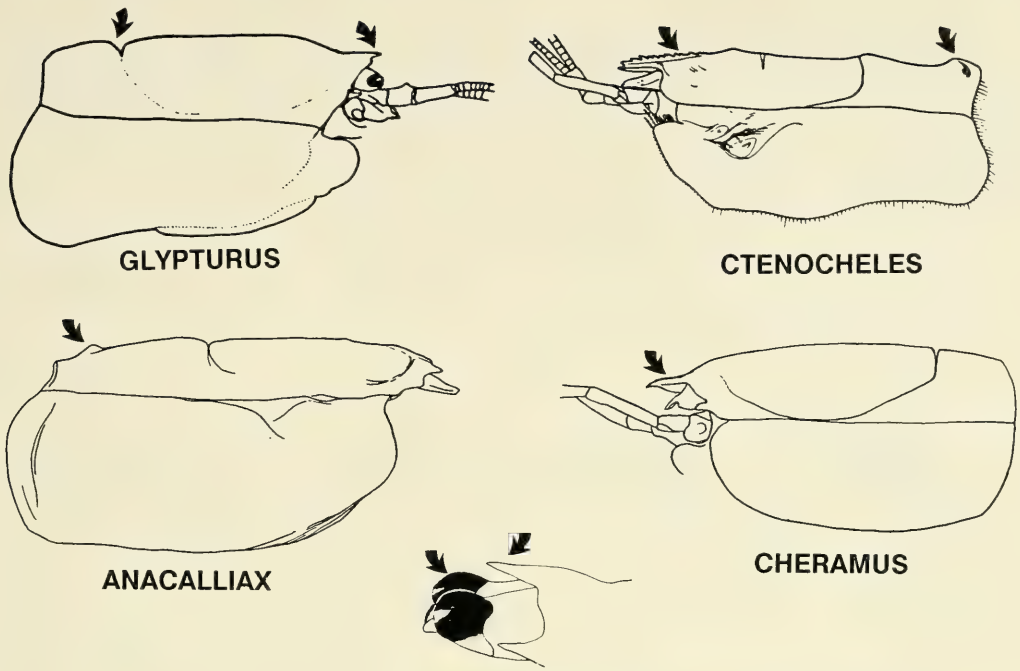


Fig. 2. Features of the carapace in some callianassid and ctenochelid genera. *Anacalliax: A. argentinensis* (Biffar), female holotype, cl 26.5 mm, Argentina, USNM 135055; *Cheramus: C. marginatus* (Rathbun), female syntype, cl 3.4 mm, Puerto Rico, USNM 23778; *Corallianassa: C. xuthua* Manning (from Manning 1988: fig. 2b); *Ctenocheles: Ctenocheles serrifrons* (Le Loeuff & Intès) (from Le Loeuff & Intès 1974: fig. 3b); *Glypturus: G. acanthochirus* (Stimpson) (from Manning 1987: fig. 3b).

(Montagu, 1808) is known from the Mediterranean and the eastern Atlantic (De Saint Laurent & Bozic 1976, De Saint Laurent & Le Loeuff 1979). Kensley (1974) named a subspecies, *C. subterranea australis,* from the west coast of South Africa. All live sublittorally.

Callianassa does not occur in the Americas, and we suspect that most, if not all, other species from outside the eastern Atlantic now placed in it should be referred to other genera.

Biffarius, new genus
Fig. 9

Type species.—*Callianassa biformis* Biffar, 1971b.

Diagnosis.—Carapace lacking rostral spine. Cornea dorsal, subterminal, flattened. A1 peduncle not longer and stouter than A2 peduncle. Mxp3 without exopod, ischium-merus operculiform; merus not projecting beyond articulation with carpus. Chelipeds unequal, major cheliped with meral hook. Plp1 vestigial or absent in male, uniramous in female; Plp2 vestigial or absent in male, biramous in female; Plp3–5 foliaceous, with stubby, projecting appendices internae in both sexes.

American species.—Two, *Biffarius biformis* (Biffar, 1971b) and *Biffarius fragilis* (Biffar, 1970), both from the northwestern Atlantic.

Remarks.—The other genera of the Callianassinae differ from *Biffarius* as follows: *Callianassa* has a pediform Mxp3, *Neotrypaea* and *Trypaea* have the merus of Mxp3 projecting beyond its articulation with the carpus, and *Notiax* has a distinct rostral spine.

Biffarius contains nearshore species of ex-

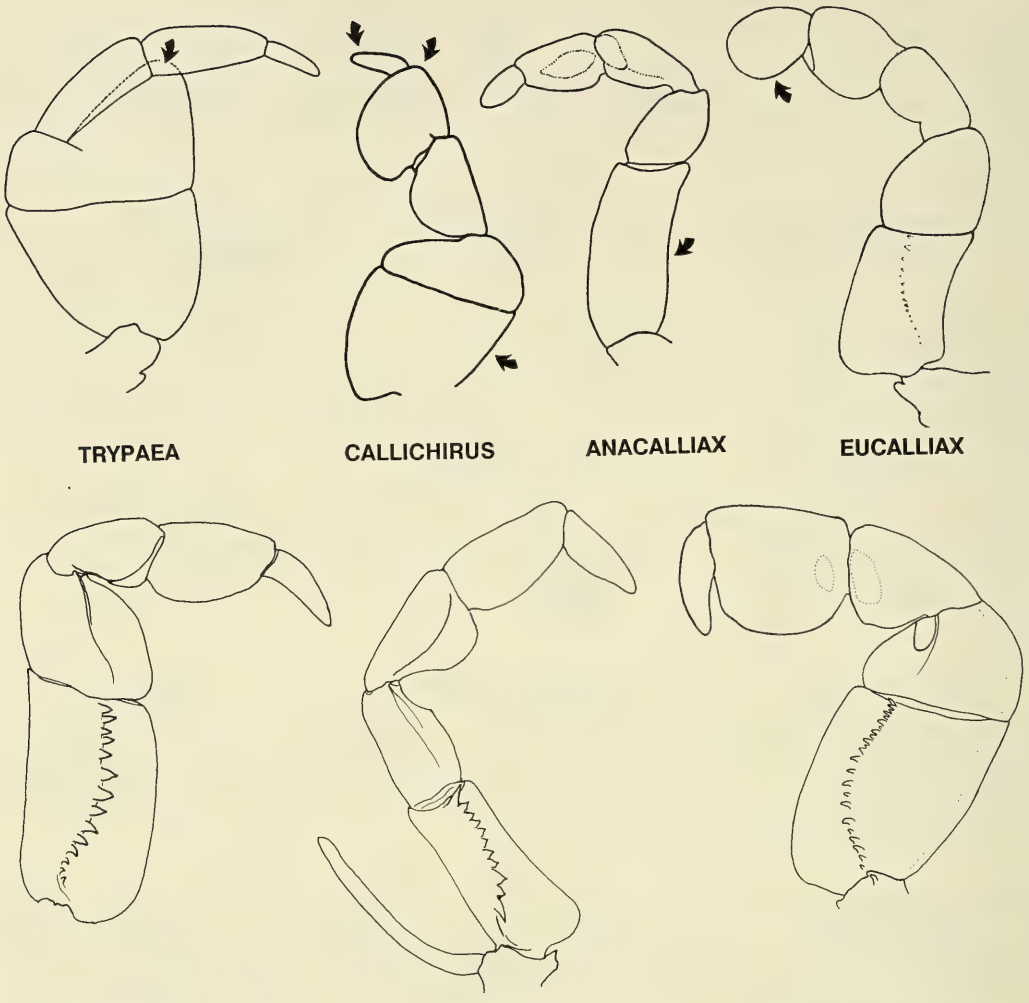


Fig. 3. Third maxillipeds of different callianassid and ctenochelid genera (form of ischium-merus in parentheses after generic name). *Anacalliax* (pediform): *A. argentinensis* (Biffar), female holotype, cl 26.5 mm, Argentina, USNM 135055; *Callianassa* (pediform): *C. subterranea* (Montagu), male, cl 12.0 mm, Scotland, USNM 252395; *Calliax* (subpediform): *C. lobata* (De Gaillande & Lagardère) (from De Saint Laurent & Bozic 1976: fig. 15); *Callichirus* (operculiform): *C. major* (Say) (from Manning & Felder 1986: fig. 1b); *Gourretia* (pediform): *G. denticulata* (Lutze), female, cl 4.5 mm, Israel, USNM 221976; *Neocallichirus* (subpediform): *N. grandimana* (Gibbes), male, cl 11.5 mm, Florida, USNM 252392; *Trypaea* (operculiform): *T. australiensis* Dana (from Poore & Griffin 1979: fig. 20f).

tremely small size, with adults no larger than 50 mm, often as small as 20 mm.

Etymology.—We dedicate this genus to Thomas A. Biffar, whose studies of the American callianassids have materially aided this review. The gender is masculine.

Calliapagurops De Saint Laurent, 1973

Calliapagurops De Saint Laurent, 1973:515. Type species *Calliapagurops charcoti* De Saint Laurent, 1973, by original designation and monotypy. Gender masculine.

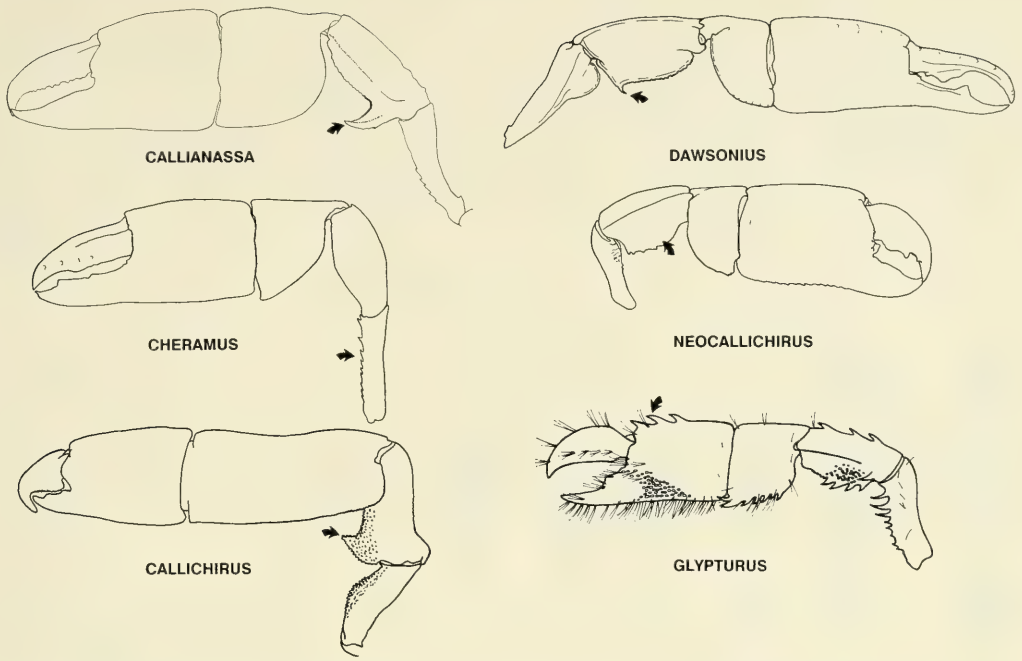


Fig. 4. Representative major chelipeds of some callianassid and ctenochelid genera. *Callianassa: C. subterranea* (Montagu), male, cl 12.0 mm, Scotland, USNM 252395; *Callichirus: C. major* (Say) (from Manning & Felder 1986: fig. 1c); *Cheramus: C. marginatus* (Rathbun), female syntype, cl 3.4 mm, Puerto Rico, USNM 23778; *Dawsonius: D. latispina* (Dawson), male holotype, cl 14.7 mm, Gulf of Mexico, USNM 105398; *Glypturus: G. acanthochirus* (Stimpson) (from Biffar 1971a: fig. 4b); *Neocallichirus: N. grandimana* (Gibbes) (from Manning 1987: fig. 2f).

Diagnosis.—Eye cylindrical, cornea terminal. Mxp3 merus with 3–4 antero-internal spines. P1 carpus as wide as merus.

American species.—None.

Remarks.—Monotypic. The unique holotype of *Calliapagurops charcoti,* known from the Azores in 190–230 m, has not been described in detail or illustrated. *Calliapagurops* apparently resembles *Scallasis* Bate (q.v.) in having a terminal cornea and it may well belong in the Cheraminae with that genus.

Neotrypaea, new genus
Fig. 10

Type species.—*Callianassa californiensis* Dana, 1854.

Diagnosis.—Carapace lacking rostral spine. Cornea dorsal, subterminal, disk-shaped. A1 peduncle longer and stouter than A2 peduncle. Mxp3 without exopod, ischium-merus operculiform; merus projecting beyond articulation with carpus. Chelipeds unequal, major with meral hook. Plp1–2 vestigial or absent in male, Plp1 uniramous and Plp2 biramous in female, lacking appendices internae; Plp3–5 foliaceous with appendices internae stubby, embedded in endopod in both sexes.

American species.—Four, *Neotrypaea uncinata* (H. Milne Edwards, 1837), *Neotrypaea gigas* (Dana, 1852), *Neotrypaea californiensis* (Dana, 1854), and *Neotrypaea affinis* (Holmes, 1900), all from the eastern Pacific.

Remarks.—*Neotrypaea* agrees with the Australian *Trypaea* and differs from the other American genera with operculiform ischium-merus on Mxp3, *Biffarius* and *No-*

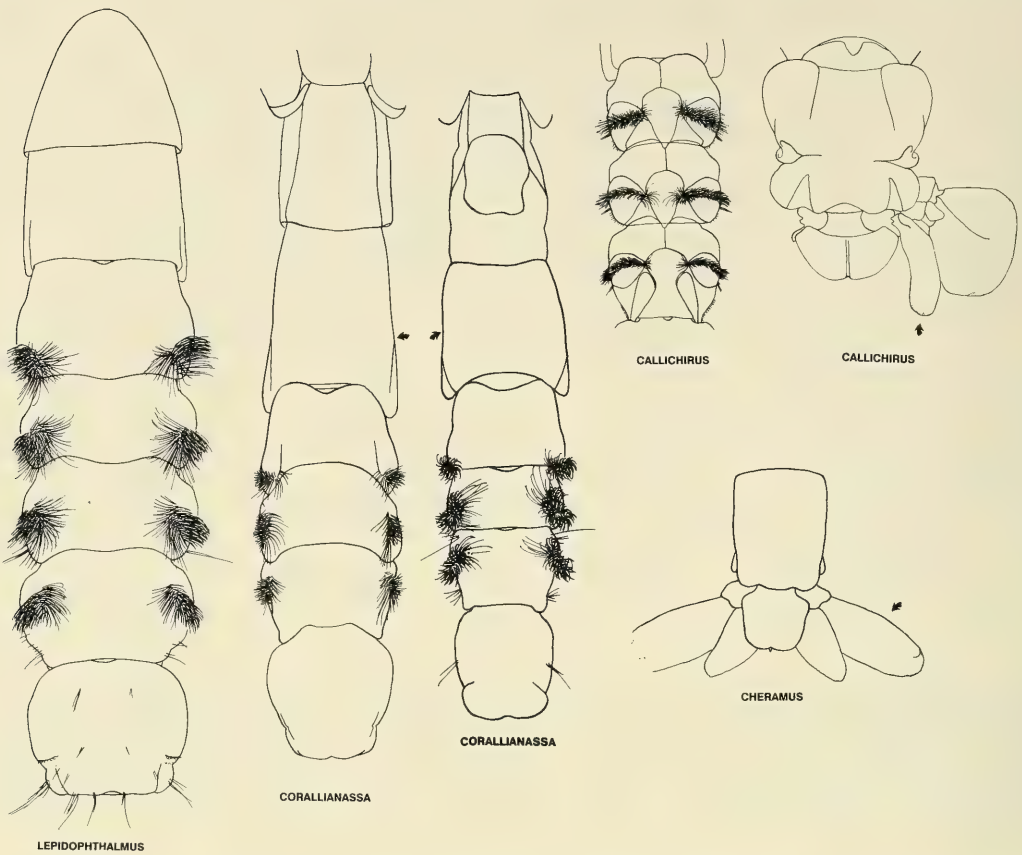


Fig. 5. Diagnostic features of the abdomen and tail fan of some callianassid and ctenochelid genera. *Callichirus: C. major* (Say), third to fifth abdominal somites (from Manning & Felder 1986: fig. 1f) and sixth abdominal somite, telson, and uropod (from Manning & Felder 1986: fig. 1e); *Cheramus: C. marginata* (Rathbun), female syntype, cl 3.4 mm, Puerto Rico, USNM 23778; *Corallianassa: C. borradailei* (De Man) (from Manning 1988: fig. 9g) and *C. xutha* Manning (from Manning 1988: fig. 3h); *Lepidophthalmus: L. jamaicense* (Schmitt), male holotype, cl about 12 mm, Jamaica, USNM 69363.

tiax, in having the A1 peduncle both longer and stouter than the A2 peduncle as well as in having the merus of Mxp3 project beyond its articulation with the carpus. The appendices internae on Plp3–5 are embedded in the margin of the endopod in members of *Neotrypaea,* projecting in members of *Trypaea.*

Known members of the genus prefer substrates ranging from clean quartzite sand beneath intertidal boulders to intertidal and subtidal combinations of mud and sand, in some cases including margins and tidal bars of inlets and sloughs or bay bottoms to depths of about 40 meters.

Etymology.—Formed by the combination of the Greek prefix *neo-*, new, and the generic name *Trypaea.* The gender is feminine.

Notiax, new genus
Figs. 6, 11

Type species.—*Callianassa brachyophthalma* A. Milne Edwards, 1870, by present designation and monotypy.

Diagnosis.—Carapace with rostral spine. Cornea dorsal, subterminal, disk-shaped. A1 peduncle not longer and stouter than A2 peduncle. Mxp3 without exopod, ischium-

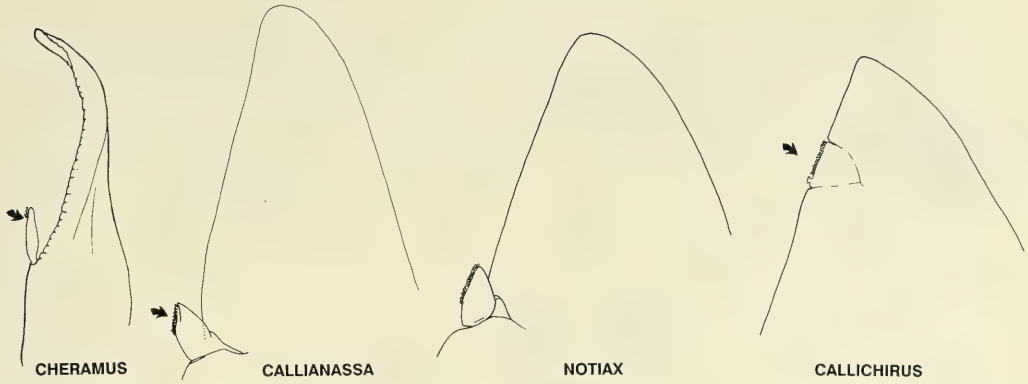


Fig. 6. Form of appendix interna on Plp3 in some genera of callianassids and ctenochelids. *Callianassa* (stubby, projecting): *C. subterranea* (Montagu), male, cl 12.0 mm, Scotland, USNM 252395; *Callichirus* (stubby, embedded): *C. seilacheri* (Bott), male, cl 24.4 mm, Peru, USNM 142540; *Cheramus* (finger-like): *C. marginatus* (Rathbun), male, cl 4.7 mm, Caribbean Sea, USNM 252397; *Notiax* (stubby, projecting): *N. brachyophthalma* (A. Milne Edwards), male, cl 16.8 mm, Chile, USNM 252309.

merus operculiform; merus not projecting beyond articulation with carpus. Chelipeds unequal, major with meral hook. Plp1 slender and uniramous, Plp2 slender and biramous, lacking an appendix interna, Plp3–5 foliaceous with stubby, projecting appendices internae in both sexes (Fig. 6).

American species.—One, *Notiax brachyophthalma* (A. Milne Edwards, 1870), from Chile and Argentina.

Remarks.—Monotypic. *Notiax* is the only American genus in which the ischium-merus of Mxp3 is operculiform which also has a rostral spine. *Trypaea* also has a rostral spine, but differs in having a much heavier A1 peduncle and in having the merus of

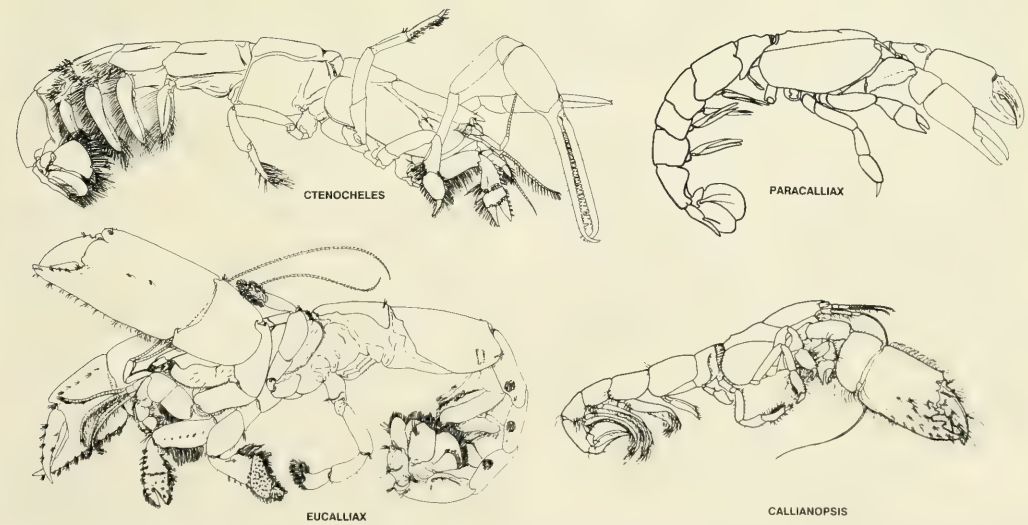


Fig. 7. Habitus of some callianassid and ctenochelid genera. *Callianopsis: C. goniophthalma* (Rathbun) (modified from Hart 1982: fig. 13a); *Ctenocheles: C. leviceps* Rabalais (from Rabalais 1979: fig. 2); *Eucalliax: E. jonesi* (Heard) (from Heard 1989: fig. 1); *Paracalliax: P. bollorei* De Saint Laurent (from De Saint Laurent & Le Loeuff 1979: fig. 26a).

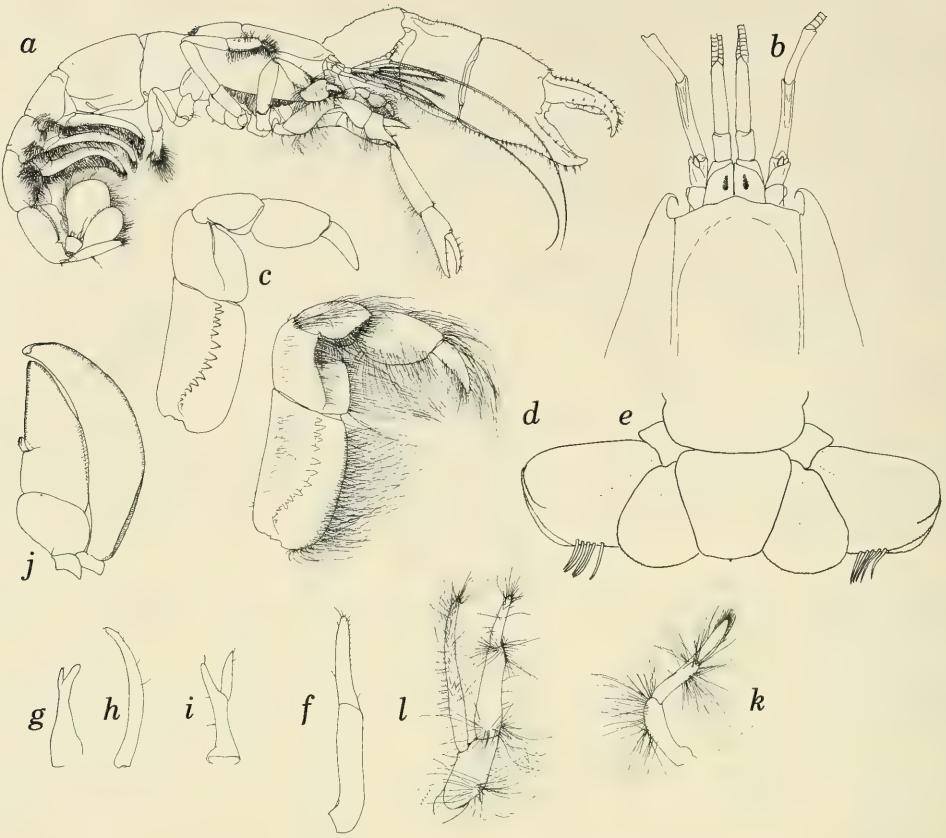


Fig. 8. *Callianassa subterranea* (Montagu). a, Lateral view; b, Anterior region of carapace and cephalic appendages, dorsal view; c, Mxp3, inner surface (setae omitted); d, Mxp3, inner surface (with setae); e, Telson and uropods; f, Male Plp1; g, Male Plp2; h, Female Plp1; i, Female Plp2; j, Female Plp3; k, Female Plp1; l, Female Plp2. a–d, f,g, male, cl 12.0 mm, Scotland, USNM 252395; e, male, cl 4.3 mm, Adriatic Sea, USNM 252396; h–j, intersex, cl 9.5 mm, Irish Sea, USNM 252394; k,l, female, cl 9.6 mm, Irish Sea, USNM 252394.

Mxp3 project beyond its articulation with the carpus.

The single known American species appears to occur subtidally in fine sand with organic debris or in mud.

Holthuis (1952) and Ferrari (1981) provided accounts of *N. brachyophthalma.*

Etymology.—From the Greek, *notios,* southern and the suffix *–ax.* The gender is feminine.

Trypaea Dana, 1852
Figs. 1, 3, 12

Trypaea Dana, 1852:14. Type species *Trypaea australiensis* Dana, 1852, by original designation and monotypy. Gender feminine.

Diagnosis.—Carapace with rostral spine. Cornea dorsal, subterminal, disk-shaped. A1 peduncle longer and stouter than A2 peduncle. Mxp3 without exopod; ischium-merus operculiform; merus projecting beyond articulation with carpus. Chelipeds unequal, major with meral hook. Plp1 uniramous and slender in both sexes; Plp2 lacking appendix interna, biramous and slender in female, absent in male; Plp3–5 foliaceous and biramous in both sexes, with stubby, projecting appendices internae.

American species.—None.

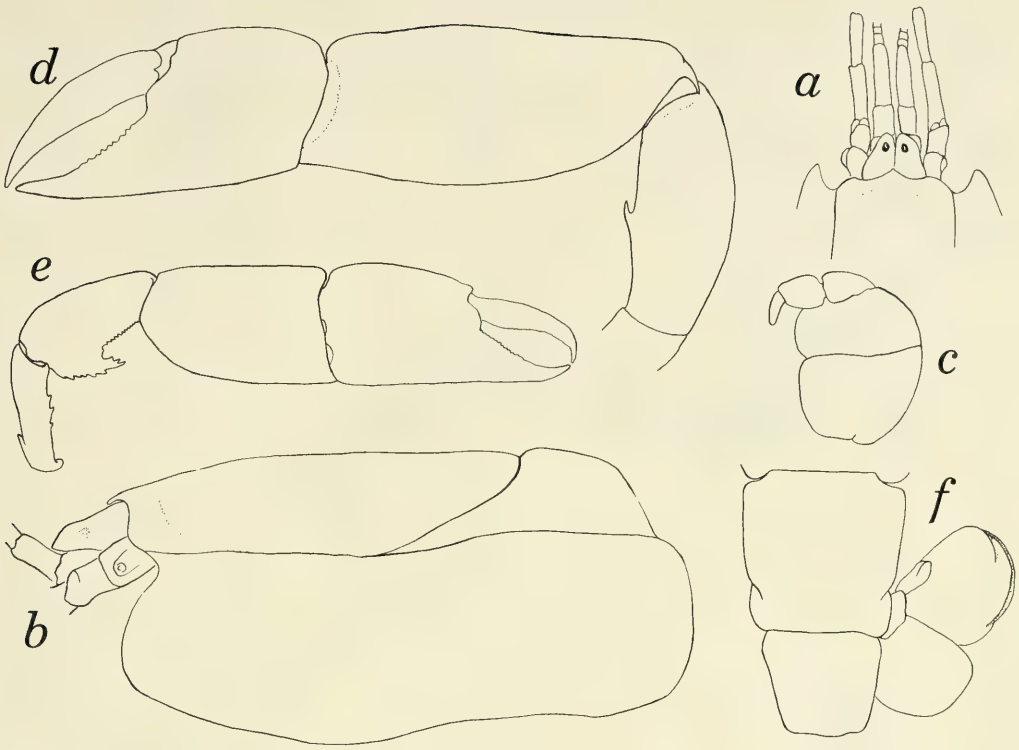


Fig. 9. *Biffarius biformis* (Biffar). a, Anterior region of carapace and cephalic appendages, dorsal view; b, Carapace and cephalic appendages, lateral view; c, Mxp3, inner surface; d, Major cheliped; e, Minor cheliped (loose in vial); f, Sixth abdominal somite, telson, and right uropod. Male, cl 3.4 mm, Florida, USNM 252391.

Remarks.—Monotypic.

Known populations prefer intertidal sand bars and mudflats, including those in estuarine settings.

Callichirinae, new subfamily

Diagnosis.—Carapace with dorsal oval. Mxp3 subpediform or operculiform, propodus ovate, dactylus slender. Plp3–5 with stubby appendices internae.

Type genus.—*Callichirus* Stimpson, 1866.

Callichirus Stimpson, 1866
Figs. 1, 3–6

Callichirus Stimpson, 1866:47. Type species *Callianassa major* Say, 1818, by original designation and monotypy. Gender masculine.

Diagnosis.—Carapace lacking rostral spine. Cornea dorsal, subterminal, disk-shaped. A1 peduncle longer and stouter than A2 peduncle. Mxp3 without exopod, ischium-merus operculiform; merus not projecting beyond articulation with carpus. Chelipeds unequal (in adult males), major with meral hook. Strong pattern of grooves and integumental glands visible dorsally on abdominal somites 3–5. Plp1 slender and uniramous, Plp2 slender and biramous, Plp3–5 foliaceous in both sexes; Plp2 with appendix interna in female embedded and distal; appendices internae stubby, embedded in margin of endopod on Plp3–5 in both sexes (Fig. 6). Uropodal endopod strap-shaped, much longer than wide.

American species.—Four, *Callichirus islagrande* (Schmitt, 1935) and *Callichirus major* (Say, 1818), from the western Atlantic and *Callichirus seilacheri* (Bott, 1955)

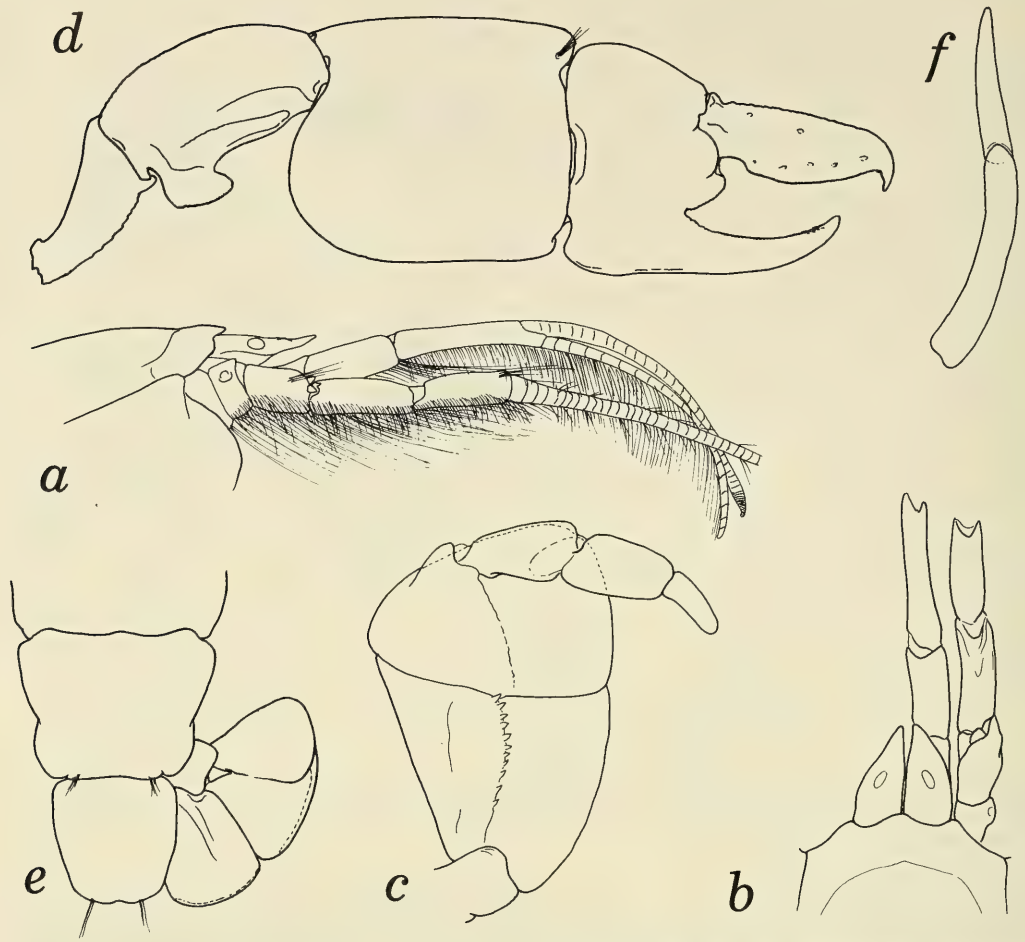


Fig. 10. *Neotrypaea californiensis* (Dana). a, Anterior region of carapace and right cephalic appendages, lateral view; b, Anterior region of carapace and cephalic appendages, dorsal view; c, Mxp3, inner surface; d, Major cheliped; e, Sixth abdominal somite, telson, and right uropod; f, Male Plp1. Male, cl 20.8 mm, California, USNM 53577.

and *Callichirus garthi* (Retamal, 1975) from the eastern Pacific.

Remarks.—As we have pointed out (Manning & Felder 1986), the dorsal cuticular pattern on the abdomen (Fig. 5) and the strap-shaped uropodal endopods (Fig. 5) are diagnostic for this genus.

Chelipeds of adult males are very unequal, whereas those of females and immatures are nearly equal. In addition, sexually mature males have a very elongate carpus on the major cheliped.

The genus includes an extralimital species, *Callichirus adamas* (Kensley, 1974), from West Africa and the west coast of South Africa.

Callichirus contains intertidal and shallow sublittoral species, most of which prefer fine, siliceous sand substrates of beaches and shallow bars. However, *C. adamas* has been reported from depths exceeding 10 meters in fine mud and silt substrates.

Corallianassa Manning, 1987
Figs. 1, 2, 5

Corallianassa Manning, 1987:392. Type species *Callianassa longiventris* A. Milne

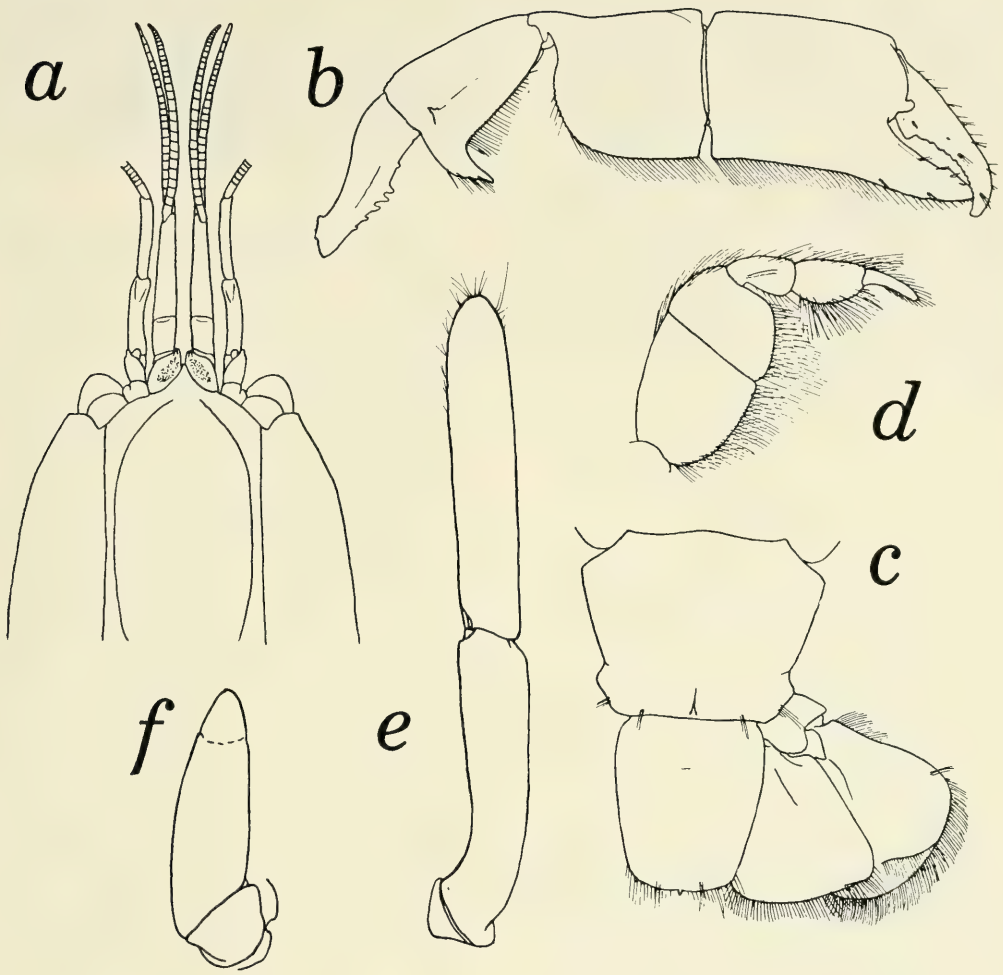


Fig. 11. *Notiax brachyophthalma* (A. Milne Edwards). a, Anterior region of carapace and cephalic appendages, dorsal view; b, Major cheliped; c, Sixth abdominal somite, telson, and right uropod; d, Mxp3, outer surface; e, Male Plp1; f, Male Plp2. a–d from Holthuis (1952: fig. 19a, b, e, f); e, f, male, cl 16.8 mm, Chile, USNM 252309.

Edwards, 1870, by original designation. Gender feminine.

Diagnosis.—Carapace with rostral spine (anterior margin of carapace with 3 spines, median extending to cornea). Cornea subglobular, appearing terminal. A1 peduncle not longer and stouter than A2 peduncle. Mxp3 without exopod, ischium-merus subpediform; merus not projecting beyond articulation with carpus. Chelipeds unequal, major lacking meral hook. Plp1 slender and uniramous, Plp2 slender and biramous, Plp3–5 foliaceous and biramous in both sexes; appendices internae finger-like and distal on Plp2, stubby, projecting on Plp3–5 in both sexes.

American species.—Three, *Corallianassa longiventris* (A. Milne Edwards, 1870), *C. hartmeyeri* (Schmitt, 1935), from Jamaica and Ascension Island (Manning & Chace 1990) and *C. xutha* Manning, 1988, from the eastern Pacific.

Remarks.—*Corallianassa* resembles *Glypturus* in having three strong anterior spines on the carapace. It differs from *Glypturus* in having a much larger, subglobular

cornea and in lacking dorsal spines on the propodus of the cheliped.

Corallianassa is represented in the Indo-West Pacific by *C. placida* (De Man, 1905) and *C. borradailei* (De Man, 1928a).

Whereas the well-formed cornea appears to be situated terminally in members of this genus, it falls short of a flange-like ventral extension of the stalk.

Species appear to prefer carbonate muds or coralline sands and may burrow in fragments of coral rubble, from the lower intertidal to a depth of several meters.

Glypturus Stimpson, 1866
Figs. 2, 4

Glypturus Stimpson, 1866:46. Type species *Glypturus acanthochirus* Stimpson, 1866, by monotypy. Gender masculine.

Diagnosis.—Carapace with rostral spine (anterior margin of carapace with 3 spines, median extending to cornea). Cornea dorsal, subterminal, disk-shaped. A1 peduncle not longer and stouter than A2 peduncle. Mxp3 without exopod, ischium-merus subpediform; merus not projecting beyond articulation with carpus. Chelipeds unequal, major without meral hook; palm with 3 spines on upper margin. Plp1 slender and uniramous, Plp2 slender and biramous, Plp3–5 foliaceous and biramous in both sexes; appendices internae finger-like on Plp2 in both sexes, stubby, projecting from endopod of Plp3–5 in both sexes.

American species.—One, *Glypturus acanthochirus* Stimpson, 1866, from the western Atlantic.

Remarks.—The trispinous front, well-formed cornea, and palm of the cheliped with 3 dorsal spines are diagnostic for the genus.

We follow Poore & Suchanek (1988) in recognizing three species in the Indo-West Pacific: *G. armatus* (A. Milne Edwards, 1870), *G. laurae* (De Saint Laurent, 1984) (in De Vaugelas & De Saint Laurent 1984), and *G. motupore* Poore & Suchanek, 1988.

Known members of the genus prefer carbonate substrates of lagoons and leeward sand flats adjacent to coral reefs, often including intertidal and subtidal areas occupied by seagrass, from shore to depths of about 30 meters.

Lepidophthalmus Holmes, 1904
Figs. 5, 13

Lepidophthalmus Holmes, 1904:310. Type species *Lepidophthalmus eiseni* Holmes, 1904, a subjective junior synonym of *Callianassa bocourti* A. Milne Edwards, 1870, by monotypy. Gender masculine.

Diagnosis.—Carapace with rostral spine. Cornea dorsal, subterminal, disk-shaped. A1 peduncle longer and stouter than A2 peduncle. Mxp3 with minute exopod, ischium-merus subpediform; merus not projecting beyond articulation with carpus. Chelipeds unequal, major with meral hook. Plp1 slender and uniramous, Plp2 slender and biramous, Plp3–5 foliaceous and biramous in both sexes; appendices internae digitiform and distal on Plp2, stubby, embedded in margin of endopod on Plp3–5 in both sexes.

American species.—Four, of which three, *Lepidophthalmus jamaicense* (Schmitt, 1935), *Lepidophthalmus louisianensis* (Schmitt, 1935), and *L. sinuensis* Lemaitre & Rodrigues, 1991 are from the western Atlantic and one, *Lepidophthalmus bocourti* (A. Milne Edwards, 1870), is known from the eastern Pacific.

Remarks.—*Lepidophthalmus* is the only member of the Callichirinae with an exopod on Mxp3; the exopod is so small that it can easily be overlooked, as it was by us initially.

Lepidophthalmus and *Callichirus* are the only two genera of the Callichirinae that also share an A1 peduncle that is both longer and stouter than the A2 peduncle. *Lepidophthalmus* has a rostral spine and lacks both the dorsal cuticular pattern on the abdomen and the strap-shaped uropodal endopods of *Callichirus*.

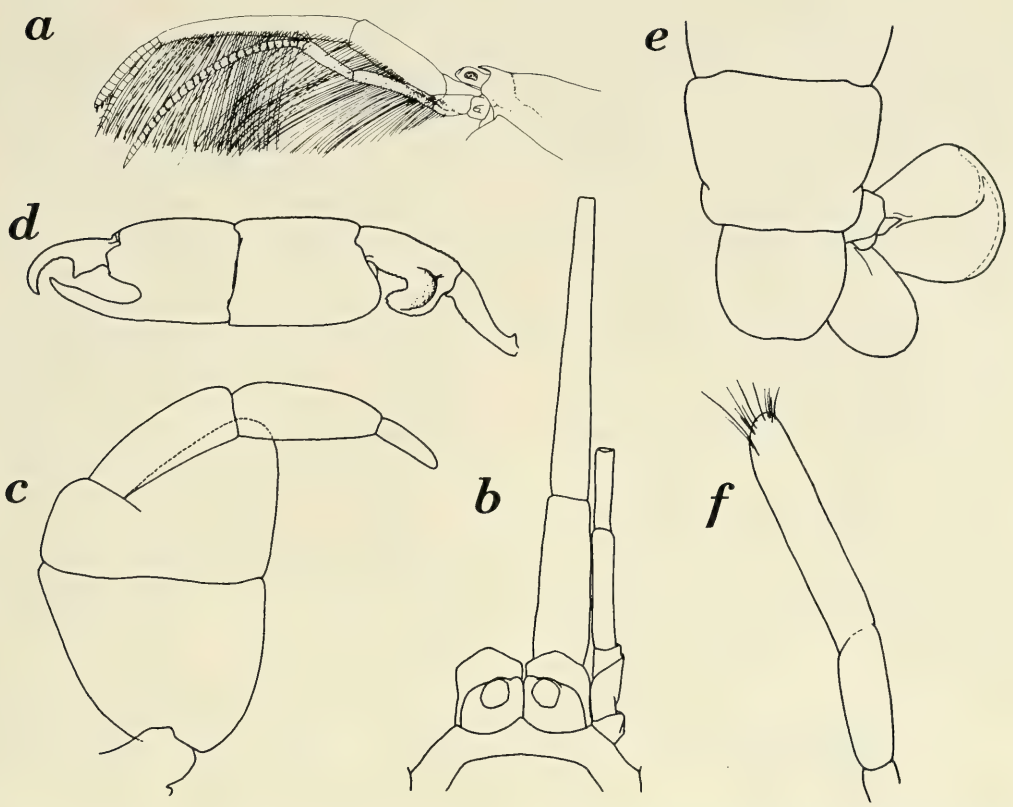


Fig. 12. *Trypaea australiensis* Dana. a, Anterior region of carapace and right cephalic appendages, lateral view; b, Anterior region of carapace and cephalic appendages, dorsal view; c, Mxp3, inner surface; d, Major cheliped; e, Sixth abdominal somite, telson, and right uropod; f, Male Plp1. a–d from Poore & Griffin (1979: figs. 18a, f, 19a, 20f); e, f male, cl 11.9 mm, Queensland, USNM 105368.

Known members of *Lepidophthalmus* all appear to be estuarine-adapted with a well developed ability for osmoregulation and an abbreviated larval life history involving two or fewer zoeal stages.

Neocallichirus Sakai, 1988
Figs. 1, 3, 4

Neocallichirus Sakai, 1988:61. Type species *Neocallichirus horneri* Sakai, 1988, by original designation. Gender masculine.

Diagnosis.—Carapace lacking rostral carina. Cornea dorsal, subterminal, disk-shaped. A1 peduncle not longer and stouter than A2 peduncle. Mxp3 without exopod, ischium-merus subpediform; merus not projecting beyond articulation with carpus. Chelipeds unequal, major without meral hook. Plp1 slender and uniramous, Plp2 slender and biramous, Plp3–5 foliaceous and biramous in both sexes; appendices internae present on Plp2 in female only, on Plp3–5 in both sexes: finger-like on Plp2, stubby, embedded in margin of endopod in Plp3–5.

American species.—Six, *Neocallichirus grandimana* (Gibbes, 1850) (=*Glypturus branneri* Rathbun, 1900), *Neocallichirus guara* (Rodrigues, 1971), *Neocallichirus guassutinga* (Rodrigues, 1971), *Neocallichirus mirim* (Rodrigues, 1971), *Neocallichirus rathbunae* (Schmitt, 1935), and *Neocallichirus trilobata* (Biffar, 1970), all western Atlantic.

Remarks.—*Neocallichirus* agrees with *Callichirus* and differs from the other four

genera of the Callichirinae in lacking a well developed rostral spine; it differs from *Callichirus* in lacking the dorsal cuticular pattern on abdominal somites 3–5 as well as the strap-shaped uropodal endopods. Two species, *N. guassutinga* and *N. rathbunae,* have three small spinules on the front of the carapace, but these spinules are much smaller than the three frontal spines found in members of *Corallianassa* and *Glypturus.*

Sakai (1988) assigned several Indo-West Pacific species to this genus.

All American species occur in intertidal or shallow subtidal nearshore habitats.

Cheraminae, new subfamily

Diagnosis.—Carapace with dorsal oval. Mxp3 pediform, propodus and dactylus slender. Plp3–5 with finger-like appendices internae.

Type genus.—*Cheramus* Bate, 1888.

Cheramus Bate, 1888
Figs. 2, 4–6, 14

Cheramus Bate, 1888:30.

Type species.—*Cheramus batei* Borradaile, 1903, a replacement name for the preoccupied *Cheramus occidentalis* Bate, 1888, by present designation. Gender masculine.

Diagnosis.—Carapace with rostral spine. Cornea subterminal, lateral. Mxp3 without exopod. Chelipeds unequal, major without meral hook. Plp1 slender and uniramous in both sexes; Plp2 slender and biramous in female, absent in male; Plp3–5 elongate and slender in both sexes, with finger-like appendices internae (Fig. 6). Uropodal exopod elongate, length more than twice width.

American species.—Two, *Cheramus batei* Borradaile, 1903 and *Cheramus marginatus* (Rathbun, 1901).

Remarks.—The long slender body with a relatively small thoracic region, strong rostral spine, pediform Mxp3, and extremely elongate uropods are characteristic of members of this genus.

In 1888 Bate named two separate taxa from parts of callianassids taken at the same station. One, which he named *Cheramus occidentalis,* was based on the body; the second, which he named *Callianassa occidentalis,* was based on a loose cheliped. Borradaile (1903) synonymized *Cheramus* with *Callianassa,* thus making *Cheramus occidentalis* a homonym of *Callianassa occidentalis* Stimpson, 1856 (a subjective junior synonym of *C. californiensis* Dana, 1854). Borradaile proposed *Callianassa batei* as a replacement name for *Cheramus occidentalis* Bate. We believe that Bate's *Callianassa occidentalis* and *Cheramus occidentalis* actually are based on the same species.

This genus contains species that live on the continental shelf and slope. Bate's type specimen of *Cheramus batei* was taken in a depth of 450 fm (823.5 m) in the West Indies.

The genus also includes *Cheramus orientalis* Bate, 1888 from the Arafura Sea and *Cheramus oblongus* (Le Loeuff & Intès, 1974) from West Africa.

Scallasis Bate, 1888

Scallasis Bate, 1888:34. Type species *Scallasis amboinae* Bate, 1888, by monotypy. Gender feminine.

Diagnosis.—Carapace with rostral spine, apparently lacking orbit. Cornea well-formed, terminal, subglobular. Mxp3 with exopod. Plp elongate and slender, with finger-like appendices internae.

American species.—None.

Remarks.—Monotypic, containing only *Scallasis amboinae* Bate, 1888, from Ambon, Indonesia. *Scallasis* apparently agrees with *Calliapagurops* in having a subglobular, terminal cornea, differing from all other callianassid genera.

The type of *S. amboinae,* in The Natural History Museum, London, was examined by one of us (R.B.M.) who verified that it is a member of the Cheraminae.

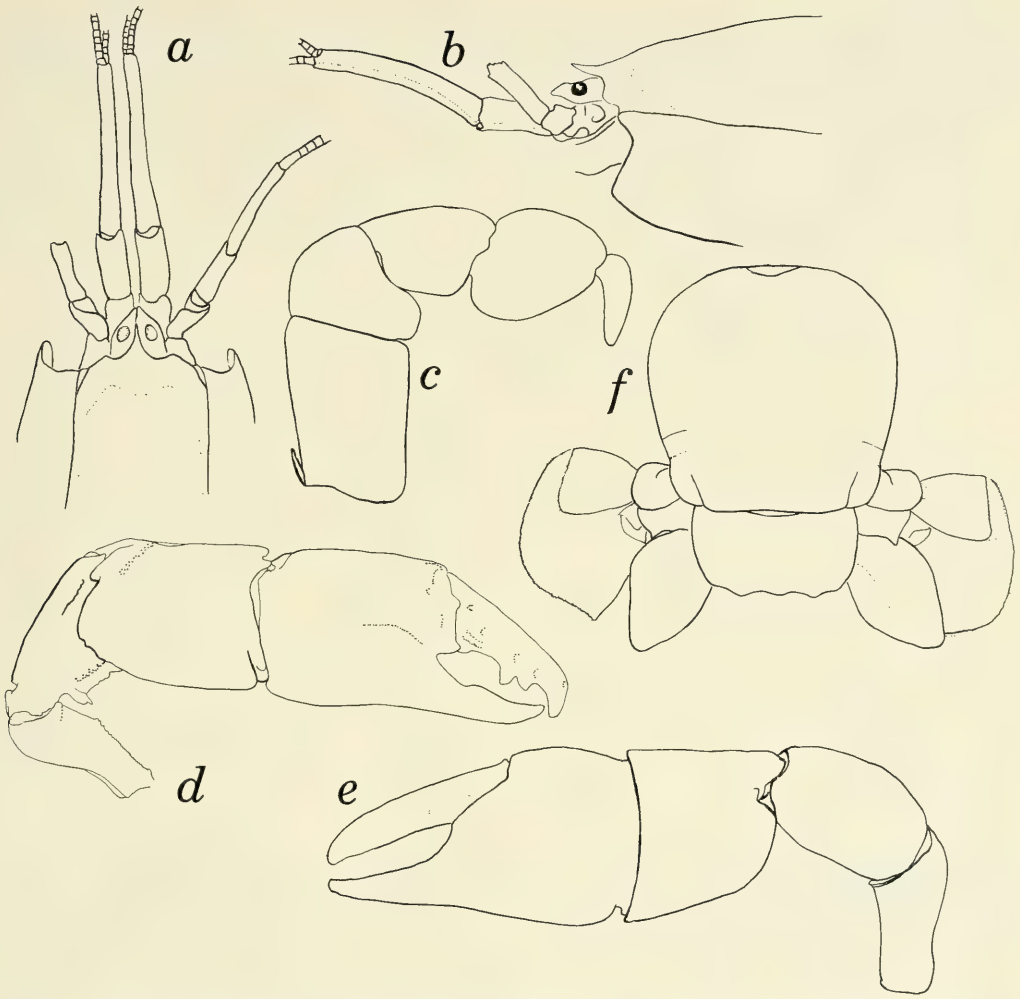


Fig. 13. *Lepidophthalmus jamaicense* (Schmitt). a, Anterior region of carapace and cephalic appendages, dorsal view; b, Anterior region of carapace and cephalic appendages, lateral view; c, Mxp3, outer surface; d, Major cheliped; e, Minor cheliped; f, Sixth abdominal somite, telson, and uropods, dorsal view. Male holotype, cl about 12 mm, Jamaica, USNM 69363.

Eucalliinae, new subfamily

Diagnosis.—Carapace lacking dorsal oval. Mxp3 propodus and dactylus ovate. Plp3–5 with finger-like appendices internae.

Type genus.—*Eucalliax,* new genus.

Eucalliax, new genus
Figs. 7, 15a–e

Type species.—*Callianassa quadracuta* Biffar, 1970.

Diagnosis.—Cornea flattened, almost terminal. Mxp3 without exopod, ischium-merus subpediform. Chelipeds equal and similar, major without meral hook. Plp1 slender and uniramous, Plp2 slender and biramous, Plp3–5 foliaceous and biramous in both Al sexes; finger-like appendices internae present on Plp2–5 in both sexes. Uropodal exopod lacking lateral notch or incision.

American species.—Two, *Eucalliax jonesi* (Heard, 1989) and *Eucalliax quadra-*

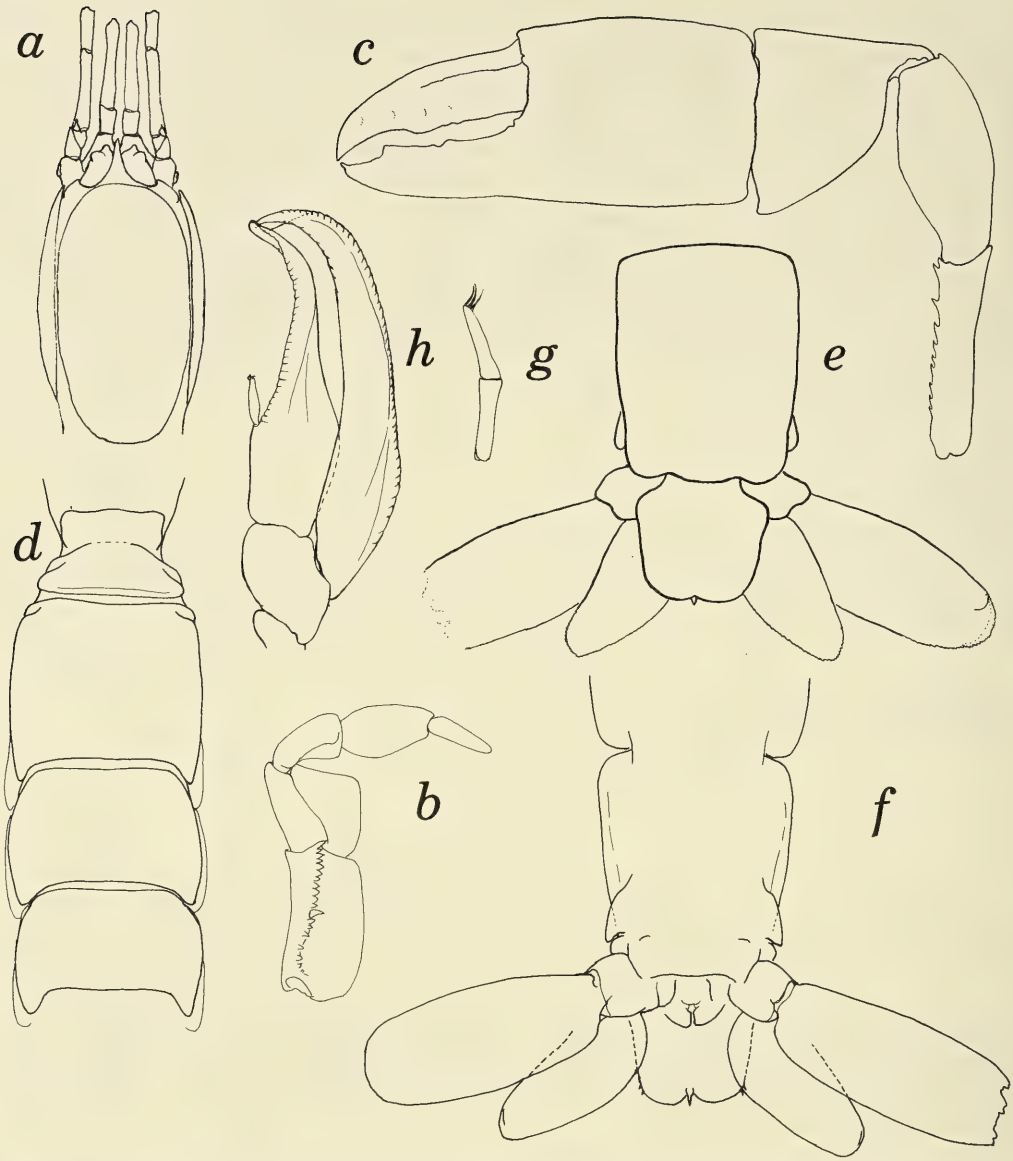


Fig. 14. *Cheramus marginatus* (Rathbun). a, Anterior two-thirds of carapace and cephalic appendages, dorsal view; b, Mxp3, inner surface; c, Major cheliped; d, Anterior 3 abdominal somites; e, Sixth abdominal somite, telson, and uropods, dorsal view; f, Sixth abdominal somite, telson, and uropods, ventral view; g, Male Plp1; h, Male Plp3. a–c, e,f, female syntype, cl 3.4 mm, Puerto Rico, USNM 23778; d, male syntype, cl 2.7 mm, Puerto Rico, USNM 24667; g,h, male, cl 4.7 mm, Caribbean Sea, USNM 252397.

cuta (Biffar, 1970), both from the northwestern Atlantic.

Remarks.—Members of *Eucalliax* differ from *Calliax* in having the chelipeds equal and similar.

Members of the genus occur in carbonate sand-silt substrates, from the intertidal to shallow subtidal depths.

Etymology.—The name is a combination of the Greek prefix *eu-*, true, and the generic name *Calliax,* selected because members of the genus agree with the original generic di-

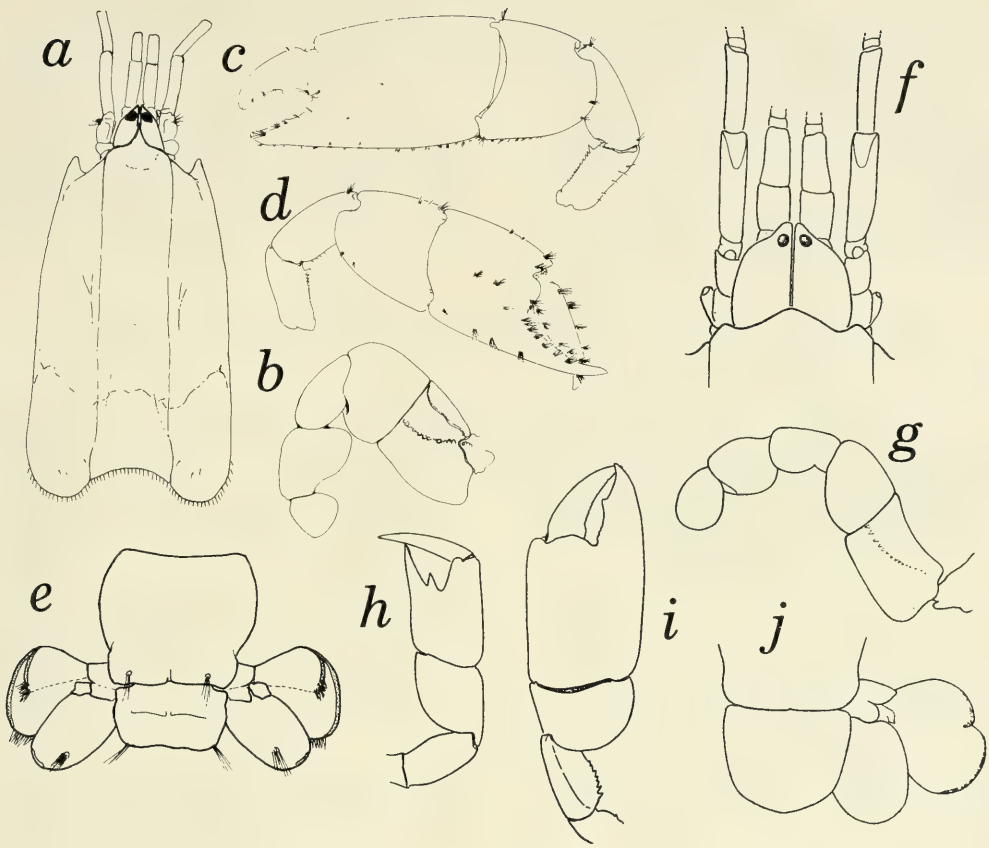


Fig. 15. Features of *Eucalliax jonesi* (Heard) (a–e) and *Calliax lobata* (De Gaillande & Lagardère) (f–j). a, Carapace and anterior cephalic appendages, dorsal view; b, Mxp3, inner surface; c, Left cheliped; d, Right cheliped; e, Sixth abdominal somite, telson, and uropods; f, Anterior region of carapace and cephalic appendages; g, Mxp3, inner surface; h, Minor cheliped; i, Major cheliped; j, Sixth abdominal, telson, and right uropod. a–e from Heard (1989: figs. 3a, 4a–c); f–j from De Saint Laurent & Bozic (1976: figs. 7, 15, 23, 34).

agnosis of equal chelae given for *Calliax*. The gender is feminine, as in *Calliax*.

Calliax De Saint Laurent, 1973
Figs. 3, 15f–j

Calliax De Saint Laurent, 1973:514. Type species *Callianassa lobata* De Gaillande & Lagardère, 1966, by original designation and monotypy. Gender feminine.

Diagnosis.—Cornea terminal, elongate. Mxp3 without exopod, ischium-merus subpediform. Chelipeds unequal, major without meral hook. Plp1 uniramous and Plp2 biramous in both sexes; Plp3–5 biramous in both sexes, type of appendices internae unknown. Uropodal exopod apparently with lateral notch or incision.

American species.—None.

Remarks.—The type species *Calliax lobata* (De Gaillande & Lagardère, 1966) is known only from the Mediterranean. In the original diagnosis of the genus the chelipeds were characterized as "habituellement subégaux" (De Saint Laurent 1973:514) in spite of the fact that they are clearly unequal and dissimilar in *C. lobata* (see De Gaillande & Lagardère 1966: fig. 2a, b and De Saint Laurent & Bozic 1976: fig. 23).

The type species lacks an exopod on

Mxp3. We believe that species with equal chelipeds and an exopod on Mxp3 assigned to *Calliax* by De Saint Laurent & Manning (1982) should be assigned to a separate new genus, an action that is beyond the scope of this study.

Members of the genus occur in a variety of shallow-water habitats.

Ctenochelidae, new family

Diagnosis.—Carapace usually with cardiac prominence. A2 with strong antennal scale. Mxp3 pediform, merus usually with distal spine. Male Plp2 with appendix masculina. Uropodal exopod longitudinally carinate dorsally, lacking dorsal plate, lateral notch or incision usually present.

Type genus.—*Ctenocheles* Kishinouye, 1926.

Included genera.—*Ctenocheles, Dawsonius,* new genus, *Gourretia,* and *Paracalliax* in the nominate subfamily, *Anacalliax* in the new subfamily Anacalliinae, and *Callianopsis* in the new subfamily Callianopsinae.

Key to American Subfamilies and Genera of Ctenochelidae

1. Carapace with dorsal oval 2
   Carapace lacking dorsal oval (Ctenochelinae) 3
2. Mxp3 dactylus ovate. Plp2–5 similar. Plp3–5 with finger-like appendices internae ..... Callianopsinae (single genus *Callianopsis*)
– Mxp3 dactylus slender, digitiform. Plp3–5 similar, with stubby appendices internae ..... Anacalliinae (single genus *Anacalliax*)
3. Cheliped with cylindrical palm, fingers much longer than palm, pectinate. Sixth abdominal somite lacking lateral projections .... *Ctenocheles*
– Cheliped with flattened palm, fingers neither elongate nor pectinate. Sixth abdominal somite with lateral projections .... *Dawsonius,* new genus

Ctenochelinae, new subfamily

Diagnosis.—Carapace lacking dorsal oval. Mxp3 propodus and dactylus slender. Plp2–5 similar, different from and larger than Plp1, with finger-like appendices internae.

Ctenocheles Kishinouye, 1926
Figs. 2, 7

Ctenocheles Kishinouye, 1926:63. Type species *Ctenocheles balssi* Kishinouye, 1926, by monotypy. Gender masculine.

Diagnosis.—Rostral carina and rostral spine present. Dorsal surface of eye flattened. Mxp3 with or without exopod, distal margin of merus usually with spine. Major cheliped with or without proximal meral hook, palm subglobular, fingers elongate, pectinate. Uropodal exopod with lateral incision.

American species.—Four, all from the western Atlantic, including two named species, *Ctenocheles holthuisi* Rodrigues, 1978, *Ctenocheles leviceps* Rabalais, 1979, and two unnamed species (*Ctenocheles* A and B) reported by Holthuis (1967).

Remarks.—Extralimital species include the type species, *C. balssi* from Japan, *C. collini* Ward, 1945 from Australia (see Poore & Griffin 1979), *C. maorianus* Powell, 1949 from New Zealand, and *C. serrifrons* Le Loeuff & Intès, 1974, and an unnamed species from West Africa (De Saint Laurent & Le Loeuff 1979).

Whereas several species, e.g., *C. serrifrons, C. holthuisi,* and *C. leviceps* have at least a vestige of an exopod on Mxp3, *C. collini* apparently lacks the exopod (see De Saint Laurent & Le Loeuff 1979:83), suggesting to us that *Ctenocheles* is a heterogeneous assemblage, including members of more than one genus. Further, *C. holthuisi,* the only member of the family that lacks a cardiac prominence on the carapace, also

differs from other species of the genus in several features, as pointed out by Rodrigues (1978).

Members of this genus are all strictly sublittoral and are found primarily from middle shelf and slope environments.

Dawsonius, new genus
Figs. 4, 16

Type species.—*Callianassa latispina* Dawson, 1967.

Diagnosis.—Carapace with rostral carina and rostral spine. Dorsal suface of eye slightly concave. Mxp3 without exopod, distal margin of merus with spine. Major cheliped with proximal meral hook. Uropodal exopod lacking lateral notch or incision.

American species.—One, *Dawsonius latispina* (Dawson, 1967), from the western Atlantic.

Remarks.—Monotypic. *Dawsonius* resembles *Gourretia* in basic facies, but differs from it in lacking an exopod on Mxp3 and in having sharp lateral projections on the sixth abdominal somite.

In his account of *D. latispina,* Biffar (1971a: fig. 11b) showed an exopod on the Mxp3 of a distinctly different species. It may prove to be a member of *Gourretia,* a genus not now known from the Americas.

Known populations occur over the continental shelf, in depths of about 10 to near 150 meters, in substrates ranging from muddy sands to soft silty clays.

Etymology.—We dedicate this genus to C. E. Dawson, who recognized the distinctness of the type species. The gender is masculine.

Gourretia De Saint Laurent, 1973
Fig. 3

Gourretia De Saint Laurent, 1973:514. Type species *Callianassa denticulata* Lutze, 1937, a junior synonym of the preoccupied *Callianassa subterranea* var. *minor* Gourret, 1887 (see Lewinsohn & Holthuis 1986), by original designation and monotypy. Gender feminine.

Diagnosis.—Carapace lacking dorsal oval and rostral carina; rostral spine usually present. Dorsal surface of eye flattened. Mxp3 with exopod; distal margin of merus usually with spine. Major cheliped with proximal meral hook. Sixth abdominal somite lacking acute lateral projections. Uropodal exopod usually lacking lateral notch or incision.

American species.—None.

Remarks.—This genus includes *G. denticulata* (Lutze) from the Mediterranean and eastern Atlantic (Le Loeuff & Intès 1974; De Saint Laurent & Bozic 1976, as *G. minor*), *G. lahouensis* Le Loeuff & Intès, 1974 and *G. barracuda* Le Loeuff & Intès, 1974, both from West Africa, an unnamed species from West Africa (De Saint Laurent & Le Loeuff 1979), and *G. coolibah* Poore & Griffin, 1979, from Australia.

Gourretia minor, G. lahouensis, and *G. barracuda* lack a lateral notch or incision on the uropodal exopod, but it is present in *G. coolibah* which, like *G. lahouensis,* also lacks the distal spine on the merus of Mxp3. Like *Ctenocheles, Gourretia* may well include representatives of more than one genus.

Members of the genus occur in shelf and slope habitats to depths of about 250 m.

Paracalliax De Saint Laurent, 1979
Figs. 1, 7

Paracalliax De Saint Laurent, 1979:1396. Type species *Paracalliax bollorei* De Saint Laurent, 1979, by original designation and monotypy.

Diagnosis.—Carapace with low rostral carina; lacking dorsal oval and rostral spine. Dorsal surface of eye concave. Mxp3 with exopod; merus with distal spine. Major cheliped lacking proximal meral hook. Sixth abdominal somite with rounded lateral pro-

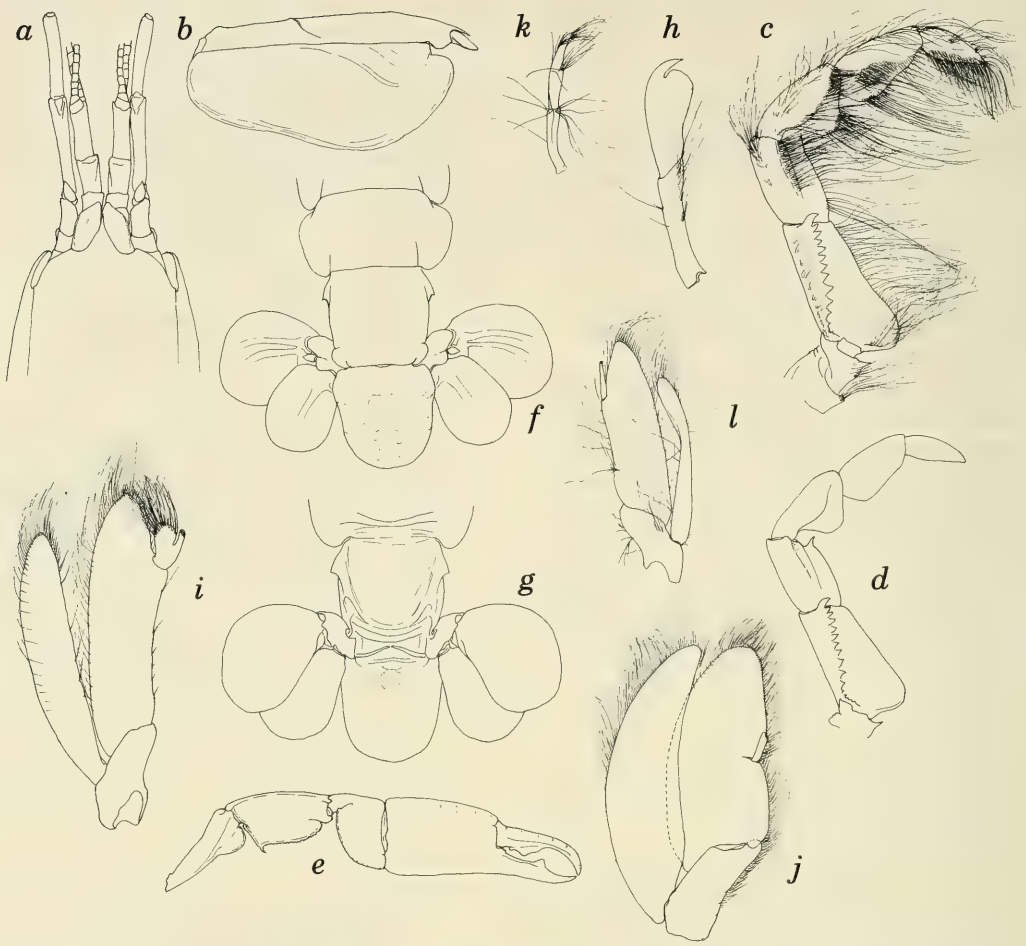


Fig. 16. *Dawsonius latispina* (Dawson). a, Anterior region of carapace and cephalic appendages, dorsal view; b, Carapace, lateral view; c, Mxp3, inner surface (with setae); d, Mxp3, inner surface (setae omitted); e, Major cheliped; f, Posterior two abdominal somites, telson, and uropods, dorsal view; g, Sixth abdominal somite, telson, and uropods, ventral view; h, Male Plp1; i, Male Plp2; j, Male Plp3; k, Female Plp1; l, Female Plp2. a–i, male holotype, cl 14.7 mm, Gulf of Mexico, USNM 105398; j, male, cl 7.9 mm, Gulf of Mexico, USNM 103755; k,l, female, cl 10.0 mm, Gulf of Mexico, USNM 252398.

jection. Uropodal exopod lacking lateral notch or incision.

American species.—None.

Remarks.—Monotypic. The unique holotype from Mauritania was described and figured by De Saint Laurent & Le Loeuff (1979).

Anacalliinae, new subfamily

Diagnosis.—Carapace with dorsal oval. Mxp3 propodus and dactylus slender. Plp3–5 similar, different from and larger than Plp1–2; Plp3–5 with appendices internae stubby, embedded in margin of endopod.

Type genus.—*Anacalliax* De Saint Laurent, 1973.

Anacalliax De Saint Laurent, 1973
Figs. 2, 3, 17

Anacalliax De Saint Laurent, 1973:515. Type species *Callianassa argentinensis* Biffar, 1971b, by original designation and monotypy.

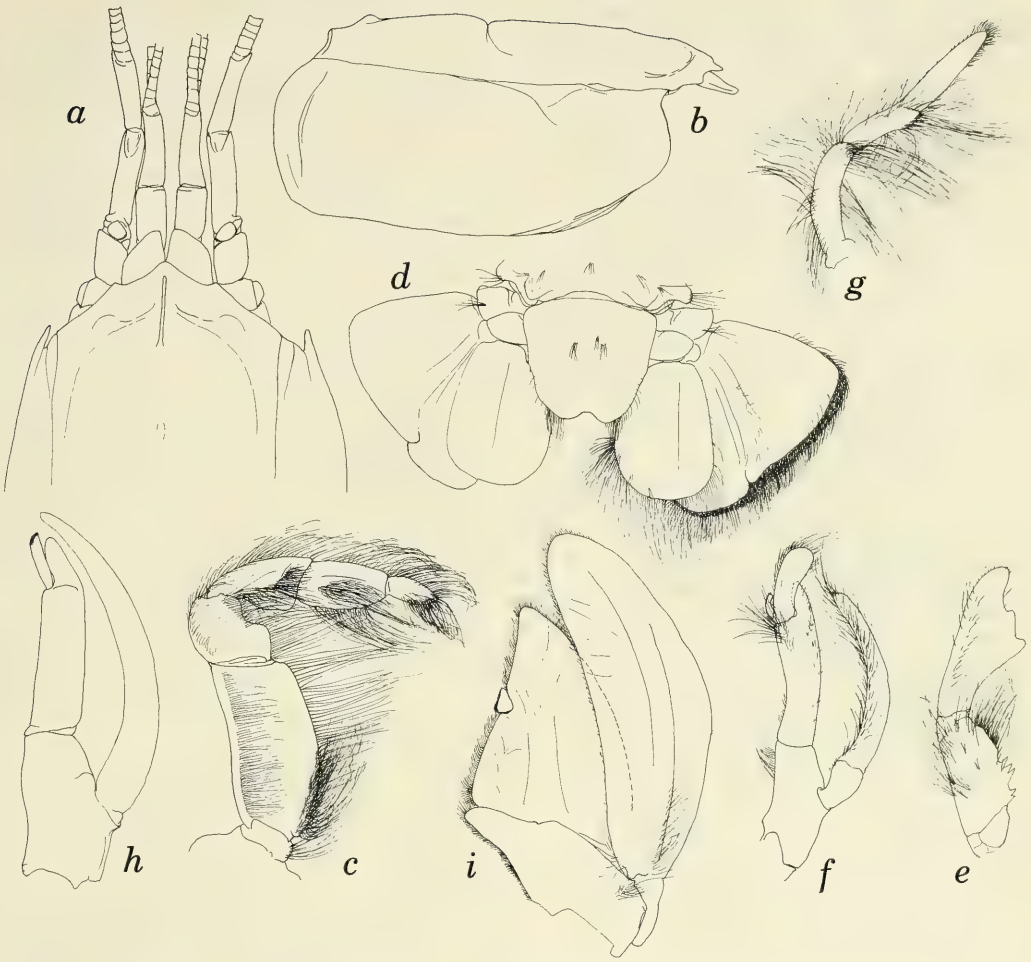


Fig. 17. *Anacalliax argentinensis* (Biffar). a, Anterior region of carapace and cephalic appendages, dorsal view; b, Carapace, lateral view; c, Mxp3, outer surface; d, Telson and uropods, dorsal view; e, Male Plp1; f, Male Plp2; g, Female Plp1; h, Female Plp2; i, Female Plp3. a–d, g–i, female holotype, cl 26.5 mm, Argentina, USNM 135055; f, g, male paratype, cl 40.9 mm, Argentina, USNM 135056.

Diagnosis.—Carapace with dorsal oval, rostral carina, and rostral spine. Cornea subterminal, indistinct. Mxp3 without exopod, ischium-merus pediform. Chelipeds unequal, major without meral hook. Plp1 slender, uniramous, Plp2 slender, biramous, Plp3–5 foliaceous in both sexes; Plp2–5 with appendices internae finger-like on Plp2, embedded in margin of endopod on Plp3–5. Uropodal exopod with lateral notch or incision.

American species.—Two, *Anacalliax agassizi* (Biffar, 1971b) and *Anacalliax argentinensis* (Biffar, 1971b), both from the Atlantic coast of South America.

Remarks.—*Anacalliax argentinensis* is known from the shallow subtidal, under stones, to the deeper sublittoral in depths of about 50 meters, in sandy mud (Biffar 1971b).

Callianopsinae, new subfamily

Diagnosis.—Carapace with dorsal oval. Mxp3 propodus and dactylus ovate. Plp2–5 similar, different from and larger than Plp1, with finger-like appendices internae.

Fig. 18. *Callianopsis goniophthalma* (Rathbun) (from Rathbun 1904: pl. 8).

Type genus.—*Callianopsis* De Saint Laurent, 1973.

Callianopsis De Saint Laurent, 1973
Figs. 7, 18

Callianopsis De Saint Laurent, 1973:515. Type species *Callianassa goniophthalma* Rathbun, 1902, by original designation and monotypy.

Diagnosis.—Carapace with dorsal oval, low rostral carina, and rostral spine. Dorsal surface of eye concave. Mxp3 without exopod; merus unarmed distally; propodus and dactylus ovate. Major cheliped with proximal meral hook. Sixth abdominal somite with acute lateral projections. Uropodal exopod lacking lateral notch or incision.

American species.—One, *Callianopsis goniophthalma* (Rathbun, 1902).

Remarks.—Monotypic. Members of this genus are known from slope depths (480–650 meters) in the northeastern Pacific.

Acknowledgments

We are indebted to the following individuals for providing comparative material: Carlo Froglia, Istituto di Ricerche sulla Pesca Marittima, Ancona, Italy; Carlos Jara, Universidad Austral de Chile; Lois Nickell, University Marine Biological Station, Millport, Scotland; and Ashley A. Rowden, Plymouth Marine Laboratory, England.

We thank our colleagues Fenner A. Chace, Jr., Brian Kensley, Austin B. Williams, and especially Sergio de Almeida Rodrigues for many helpful discussions of the importance of various characters in the ghost shrimps.

Many of the figures were executed by Lilly King Manning, who prepared all of the figures for publication.

This work was supported in part by Louisiana NSF/EPSCoR Program grant R11-8820219, U.S. Minerals Management Service Cooperative Agreement 14-35-0001-30470, funds for illustrations from the Coypu Foundation, and Louisiana Education Quality Support grants 86-LUM(1)-083-13 and (1987-88)-ENH-BS-10.

This is contribution number 281 from the Smithsonian Marine Station at Link Port, Florida, and contribution number 26 from the Center for Crustacean Research, University of Southwestern Louisiana.

Literature Cited

Bate, C. S. 1888. Report on the Crustacea Macrura collected by H.M.S. *Challenger* during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. *Challenger* during the years 1873–76, Zoology 24: xc + 942 pages, pls. 1–157.

Biffar, T. A. 1970. Three new species of callianassid shrimp (Decapoda, Thalassinidea) from the western Atlantic.—Proceedings of the Biological Society of Washington 83(3):35–49.

———. 1971a. The genus *Callianassa* (Crustacea, Decapoda, Thalassinidea) in south Florida, with keys to the western Atlantic species.—Bulletin of Marine Science 21(3):637–715.

———. 1971b. New species of *Callianassa* (Decapoda, Thalassinidea) from the western Atlantic.—Crustaceana 21(3):225–236.

Borradaile, L. A. 1903. On the classification of the Thalassinidea.—Annals and Magazine of Natural History (7)12:534–551.

Bott, R. 1955. Litorale Dekapoden, ausser *Uca*. Dekapoden (Crustacea) aus El Salvador, 2.—Senckenbergiana Biologica 36(1/2):45–70, pls. 1–8.

Dana, J. D. 1852. Macroura. Conspectus Crustaceorum &. Conspectus of the Crustacea of the Exploring Expedition under Capt C. Wilkes, U.S.N.—Proceedings of the Academy of Natural Sciences of Philadelphia 6:10–28.

———. 1854. Catalogue and descriptions of Crustacea collected in California by Dr. John L. Le Conte.—Proceedings of the Academy of Natural Sciences of Philadelphia 7:175–177.

Dawson, C. E. 1967. *Callianassa latispina* (Decapoda, Thalassinidea), a new mud shrimp from the northern Gulf of Mexico.—Crustaceana 13(2):190–196.

DeKay, J. E. 1844. Crustacea. *In* Zoology of New York, or the New-York fauna; comprising detailed descriptions of all the animals hitherto observed within the state of New-York, with brief notices of those occasionally found near its borders, and accompanied by appropriate il-

lustrations 6:1–70, plates 1–13. Carroll and Cook, Albany.

Ferrari, L. 1981. Aportes para el conocimiento de la familia Callianassidae (Decapoda, Macrura) en el Oceano Atlántico sudoccidental.—Physis, Buenos Aires, Secc. A 39(97):11–21.

Gaillande, D. de, & J.-P. Lagardère. 1966. Description de *Callianassa* (*Callichirus*) *lobata* nov. sp. (Crustacea Decapoda Callianassidae).—Recueil des Travaux de la Station Marine d'Endoume 40(56):259–265.

Gibbes, L. R. 1850. On the carcinological collections of the United States, and an enumeration of the species contained in them, with notes on the most remarkable, and descriptions of new species.—Proceedings of the American Association for the Advancement of Science, 3rd meeting: 167–201.

Gourret, P. 1887. Sur quelques Décapodes macroures nouveaux du Golfe de Marseille.—Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris 105:1033–1035.

Gurney, R. 1944. The systematics of the crustacean genus *Callianassa*.—Proceedings of the Zoological Society of London 114:82–90.

Hart, J. F. L. 1982. Crabs and their relatives from British Columbia.—British Columbia Provincial Museum, Handbook 40:266 pp.

Heard, R. W. 1989. *Calliax jonesi*, n. sp. (Decapoda: Thalassinidea: Callianassidae) from the northwestern Bahamas.—Gulf Research Reports 8(2): 129–136.

Holmes, S. J. 1900. Synopsis of California stalk-eyed Crustacea.—Occasional Papers of the California Academy of Sciences 7:263 pp.

———. 1904. On some new or imperfectly known species of west American Crustacea.—Proceedings of the California Academy of Sciences (3, Zoology) 3:307–331.

Holthuis, L. B. 1952. The Crustacea Decapoda Macrura of Chile. Reports of the Lund University Chile Expedition 1948–49, 5.—Lunds Universitets Årsskrift (N.F. Avd. 2) 47(10):1–109.

———. 1967. A survey of the genus *Ctenocheles* (Crustacea: Decapoda, Callianassidae), with a discussion of its zoogeography and its occurrence in the Atlantic Ocean.—Bulletin of Marine Science 17(2):376–385.

Kensley, B. 1974. The genus *Callianassa* (Crustacea, Decapoda, Thalassinidea) from the west coast of South Africa with a key to the South African species.—Annals of the South African Museum 62:265–278.

Kishinouye, K. 1926. Two rare and remarkable forms of macrurous Crustacea from Japan.—Annotationes Zoologicae Japonenses 11(1):63–70.

Leach, W. E. 1814. Crustaceology. *In* D. Brewster, ed., Edinburgh Encyclopaedia 7(2):385–437, Edinburgh.

Le Loeuff, P., & A. Intès. 1974. Les Thalassinidea (Crustacea, Decapoda) du Golfe de Guinée. Systématique—Écologie.—Cahiers O.R.S.T.O.M., Série Océanographique 12(1):17–69.

Lemaitre, R., & S. de A. Rodrigues. 1991. *Lepidophthalmus sinuensis*, a new species of ghost shrimp (Decapoda: Thalassinidea: Callianassidae) of importance to the culture of penaeid shrimp on the Caribbean coast of Colombia, with observations on its ecology.—Fishery Bulletin 89(4):623–630.

Lewinsohn, Ch., & L. B. Holthuis. 1986. The Crustacea Decapoda of Cyprus.—Zoologische Verhandelingen, Leiden 230:1–64.

Lutze, J. 1937. Eine neue Callianassa-Art aus der Adria.—Note dell'Istituto Italo-Germanico di Biologia Marina di Rovigno d'Istria 2(1):1–12, 1 map.

Man, J. G. de. 1905. Diagnoses of new species of macrurous decapod Crustacea from the "Siboga-Expedition."—Tijdschrift des Nederlandsche Dierkundige Vereeniging (2)9:587–614.

———. 1928a. A contribution to the knowledge of twenty-two species and three varieties of the genus Callianassa Leach.—Capita Zoologica 2(6): 1–56, pls. 1–12.

———. 1928b. The Thalassinidae and Callianassidae collected by the Siboga-Expedition with some remarks on the Laomediidae. The Decapoda of the Siboga-Expedition, Part 7.—Siboga-Expeditie, Monographe 39a6:1–187, pls. 1–20.

Manning, R. B. 1987. Notes on western Atlantic Callianassidae (Crustacea: Decapoda: Thalassinidae).—Proceedings of the Biological Society of Washington 100:386–401.

———. 1988. The status of *Callianassa hartmeyeri* Schmitt, 1935, with the description of *Coralliannassa xutha* from the west coast of America (Crustacea, Decapoda, Thalassinidae).—Proceedings of the Biological Society of Washington 101:883–889.

———, & F. A. Chace, Jr. 1990. Decapod and stomatopod Crustacea from Ascension Island, South Atlantic Ocean.—Smithsonian Contributions to Zoology 503:1–91.

———, & D. L. Felder. 1986. The status of the callianassid genus *Callichirus* Stimpson, 1866 (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington 99:437–443.

Milne Edwards, A. 1870. Révision du genre *Callianassa* (Leach) et description des plusieurs espèces nouvelles de ce groupe faisant partie de la

collection du Muséum.—Nouvelle Archives du Muséum d'Histoire Naturelle, Paris 6:75–101, pls. 1, 2.

Milne Edwards, H. 1837. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux 2: 532 pp. Paris.

Montagu, G. 1808. Description of several marine animals found on the South coast of Devonshire.—Transactions of the Linnean Society of London 9:18–114, pls. 2–8.

Poore, G. C. B., & D. J. G. Griffin. 1979. The Thalassinidea (Crustacea: Decapoda) of Australia.—Records of the Australian Museum 32(6):217–321.

———, & T. H. Suchanek. 1988. *Glypturus motopore,* a new callianassid shrimp (Crustacea: Decapoda) from Papua New Guinea with notes on its ecology.—Records of the Australian Museum 40:197–204.

Powell, A. W. B. 1949. New species of Crustacea from New Zealand of the genera *Scyllarus* and *Ctenocheles* with notes on *Lyreidus tridentatus.*—Records of the Auckland Institute and Museum 3(6): 368–371, pl. 68.

Rabalais, N. N. 1979. A new species of *Ctenocheles* (Crustacea: Decapoda: Thalassinidea) from the northwestern Gulf of Mexico.—Proceedings of the Biological Society of Washington 92:294–306.

Rathbun, M. J. 1900. The decapod and stomatopod Crustacea. Results of the Branner-Agassiz Expedition to Brazil, 1.—Proceedings of the Washington Academy of Sciences 2:135–155, pl. 8.

———. 1901. The Brachyura and Macrura of Porto Rico.—Bulletin of the United States Fish Commission, for 1900 20(2):1–127.

———. 1902. Descriptions of new decapod crustaceans from the west coast of North America.—Proceedings of the United States National Museum 24:885–905.

———. 1904. Decapod crustaceans from the northwest coast of North America.—Harriman Alaska Series 10:1–210.

———. 1926. The fossil stalk-eyed Crustacea of the Pacific slope of North America.—United States National Museum, Bulletin 138:1–155.

Retamal, M. A. 1975. Descripción de una nueva especie del género *Callianassa* y clave para reconocer las especies chilenas.—Boletín de Sociedad de Biología de Concepción 49:177–184.

Rodrigues, S. de A. 1971. Mud shrimps of the genus *Callianassa* Leach from the Brazilian coast (Crustacea, Decapoda).—Arquivos de Zoologia, São Paulo 20(3):191–223.

———. 1978. *Ctenocheles holthuisi* (Decapoda, Thalassinidea), a new remarkable mud shrimp from the Atlantic Ocean.—Crustaceana 34(2):113–120.

Saint Laurent, M. de. 1973. Sur la systématique et la phylogénie des Thalassinidea: définition des familles des Callianassidae et des Upogebiidae et diagnose de cinq genres nouveaux (Crustacea Decapoda).—Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris (series D) 277:513–516.

———. 1979. Sur la classification et la phylogénie des Thalassinides: définitions de la superfamille des Axioidea, de la sous-famille des Thomassiniinae et de deux genres nouveaux (Crustacea Decapoda).—Comptes Rendus Hebdomadaires de l'Académie des Sciences, Paris (series D) 288: 1395–1397.

———, & B. Bozic. 1976. Diagnoses et tableau de détermination des Callianasses de l'Atlantique nord oriental et de Méditerranée (Crustacea, Decapoda, Callianassidae).—Thalassia Jugoslavica 8(1) [for 1972]:15–40.

———, & P. Le Loeuff. 1979. Upogebiidae et Callianassidae. Crustacés Décapodes Thalassinidea, 1. Campagnes de la *Calypso* au large des côtes Atlantiques africaines (1956 et 1959) (suite), 22.—Résultats Scientifiques des Campagnes de la *Calypso* 11:29–101.

———, & R. B. Manning. 1982. *Calliax punica,* espèce nouvelle de Callianassidae (Crustacea, Decapoda) des eaux méditerranéennes.—Quaderni del Laboratorio di Tecnologia della Pesca, Ancona 3(2–5):211–224.

Sakai, K. 1988. A new genus and five new species of Callianassidae (Crustacea: Decapoda: Thalassinidea) from northern Australia.—The Beagle, Records of the Northern Territory Museum of Arts and Sciences 5(1):51–69.

Say, T. 1818. An account of the Crustacea of the United States [Part 5].—Journal of the Academy of Natural Sciences of Philadelphia 1 (part 2, number 1):235–253.

Schmitt, W. L. 1935. Mud shrimps of the Atlantic coast of North America.—Smithsonian Miscellaneous Collections 93(2):1–21, pls. 1–4.

Stimpson, W. 1856. On some Californian Crustacea.—Proceedings of the California Academy of Sciences 1:87–90.

———. 1866. Descriptions of new genera and species of macrurous Crustacea from the coasts of North America.—Proceedings of the Chicago Academy of Sciences 1:46–48.

Vaugelas, J. de, & M. de Saint Laurent. 1984. Premières données sur l'écologie de *Callichirus laurae* de Saint Laurent sp. nov. (Crustacé Décapode Callianassidae): son action bioturbatrice sur les formations sédimentaires du goife d'Aqa-

ba (Mer Rouge).—Comptes Rendus Hebdomadaires de Séances de l'Académie des Sciences, Paris (series 3) 298:147–152.

Ward, M. 1945. A new crustacean.—Memoirs of the Queensland Museum 12(3):134–135, pl. 13.

(RBM) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.; (DLF) Department of Biology, University of Southwestern Louisiana, Lafayette, Louisiana 70504, U.S.A.

ADDENDUM

Callianassa rochei Bouvier (1895:7), originally described from Baja California, Mexico, is a species of uncertain position that should have been mentioned in the Introduction. Whereas it cannot be assigned to any of the genera recognized here and it cannot be identified with any of the species known from Baja California from information in the original description, it probably can be considered to be a species of *Neotrypaea,* as Bouvier noted that it presented most of the features of *N. californiensis, N. uncinata,* and *N. gigas.* The original citation is:

Bouvier, E.-L. 1895. Sur une collection de Crustacés Décapodes recueillis en Basse-Californie par M. Diguet.—Bulletin du Muséum d'Histoire Naturelle, Paris 1:6–8.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 793–799

A NEW HERMIT CRAB (DECAPODA: PAGURIDAE) FROM ROCKY SHORES OF THE OGASAWARA (BONIN) ISLANDS

Akira Asakura

Abstract.—A new species of hermit crab (Family Paguridae) from the Ogasawara (Bonin) Islands, *Pagurus insulae,* is described, illustrated, and compared with closely related species.

The Ogasawara (Bonin) Islands are subtropical oceanic islands located in the northwest Pacific (27°N, 142°E). More than 50% of the terrestrial species there are endemic, as also are several of the marine species (Shigei 1970, Habe et al. 1978).

Several investigations have been done on the marine fauna of the islands, and a number of species of hermit crabs have been recorded (Hirota 1894, Yoshiwara 1901, Stimpson 1907, Terao 1913, Melin 1939, Imajima 1970, Ooishi 1970, Sugano 1974, Takeda 1981). Among these is an undetermined species of *Pagurus* (Ooishi 1970, Shigei 1970). This is possibly the same one collected on the islands of Chichijima and Hahajima of the Ogasawara Islands during our field work in 1986 and 1989, and that is here described as *Pagurus insulae,* new species.

The terminology used herein follows that of McLaughlin (1974). The size range of the specimens are given in parentheses under "Material examined," showing the shield length (SL in mm). The type material is deposited in the Natural History Museum and Institute, Chiba (CBM).

Pagurus insulae, new species
Figs. 1, 2

Material examined.—Okumura, Sakaiura, and Toufu-iwa on Chichijima Island, Ogasawara Islands: 15 males (SL = 1.55–3.10 mm), 11 females (SL = 1.60–2.90 mm). The largest male is the holotype, CBM-ZC-00711. Shells; *Monodonta australis* Lamarck, *Diloma suavis* (Philippi), *Nodilittorina pyramidalis* (Quoy & Gaimard), *Nodilittorina quadricinta feejeensis* (Reeve), *Supplanaxis niger* (Quoy & Gaimard), *Canarium mutabilis* (Swainson), *Maculotriton serrialis* (Deshayes), *Drupa ricinus hadari* Emerson & Cernohorsky, *Telasco sufflatus* (Gould), *Telasco velatus* Gould.

Description.—Shield nearly as long as broad; anterolateral margin sloping; anterior margin between rostrum and lateral projections slightly concave; posterior margin roundly truncate; dorsal surface nearly smooth and with tufts of setae; anterolateral angle unarmed.

Rostrum moderately short, slightly exceeding lateral projections, obtusely triangular, terminating in blunt tip. Lateral projections broadly and obtusely triangular.

Ocular peduncles moderately long, one-half length of shield, somewhat inflated basally, corneae slightly dilated; dorsal and dorsomesial faces each with longitudinal row of few short setae. Ocular acicles large, subtriangular, mesial margins expanded, lateral margins broadly expanded basally, medially excavated, terminating in small acute marginal spine; separated basally by ⅔ basal width of one acicle.

Antennular peduncles short, equaling length of ocular peduncles. Ultimate segment with few distal setae. Penultimate and basal segments unarmed.

Antennal peduncles moderately short but equally as long as ocular peduncle. Fifth and

fourth segments unarmed, each with few tufts of short setae. Third segment with distoventral spine. Second segment with dorsolateral distal angle produced, terminating in acute spine, mesial margin unarmed, lateral margin with row of long setae, dorsomesial distal angle with small spine. First segment with small spine on distolateral margin.

Mandible without distinguishing characters. Maxillule with proximal endite subquadrate; endopod with strong bristle on internal lobe; external lobe obsolete. Maxilla with endopod inflated basally and slightly exceeding scaphognathite. Third maxilliped with an accessory tooth on crista dentata on ischium; merus and carpus unarmed.

Right cheliped large and elongate, length about 3.25 times that of shield. Dactyl moderately short and broad, ¾ length of palm, terminating in small corneous claw; cutting edge with row of strong calcareous teeth; dorsomesial margin with few tufts of setae and with slightly elevated longitudinal row of small spines; dorsal face with scattered, moderately strong spines and with 2 rows of tufts of stiff bristles; ventral face and ventrolateral margin with tufts of setae. Palm long, ⅔ length of carpus; dorsomesial margin with tubercles; dorsal surface with closely-spaced spines or tubercles (mainly on posterior half of palm) and moderately dense short setae; dorsolateral margin with single or double row of spines continued onto fixed finger and with scattered short setae; ventral surface with scattered, closely-spaced, blunt tubercles of various sizes and few tufts of short setae; dorso- and ventro-mesial margins of fixed finger each with rows of tufts of stiff bristles. Carpus moderately long, slightly longer than merus; dorsomesial margin with single or double row of small tubercles; dorsal surface with closely-spaced, spinulose tubercles and dense short setae; lateral, mesial, and ventral surfaces with closely-spaced tubercles and tufts of short setae. Merus subtriangular; dorsal surface with irregularly scattered low tubercles of various sizes and tufts of stiff setae; distal margin unarmed; ventromesial margin with single, irregular row of small spines; lateral face somewhat tuberculate, ventrolateral margin with irregular row of small tubercles; ventral surface with scattered small tubercles and tufts of setae. Ischium with tubercles and few short setae on ventromesial margin. Coxa with irregular row of small spines on ventromesial margin.

Left cheliped considerably shorter than right, reaching to proximal margin of right palm. Dactyl moderately long, 1.5 length of palm, slightly skewed laterad; cutting edge with row of dense corneous teeth on proximal half, terminating in strong corneous claw, slightly overlapped by fixed finger; prominent hiatus between dactyl and fixed finger; dorsomesial margin with tufts of stiff setae; dorsal surface spinulose and with scattered tufts of long setae. Palm moderately short, 4/7 length of carpus; dorsal surface with irregular rows of small spines or 2 rows of tubercles and scattered tufts of long setae; lateral, mesial, and ventral surfaces tuberculate, with tufts of long setae; fixed finger terminating in strong corneous claw. Carpus moderately long, approximately equaling length of merus; dorsal surface with 2 rows of spines and tufts of long setae; lateral face tuberculate; mesial face with few scattered, low tubercles; ventral surface tuberculate and with tufts of long setae. Merus subtriangular, dorsal surface with irregular rows of low tubercles and tufts of long setae; lateral face somewhat tuberculate; ventrolateral margin with row of small spines increasing in size distally; ventral surface with tufts of long setae distally; ventromesial margin with tufts of long setae; lateral face with scattered short setae. Ischium with row of denticles on ventromesial margin, ventral surface with tufts of long setae. Coxa with spinules on ventromesial and ventrolateral margins, distal margin with tufts of long setae.

Second pereopods moderately short, not

overreaching right cheliped. Dactyl long, slender, 4/5 length of propodus, straight in lateral and dorsal view, terminating in strong corneous claw; dorsal surface with few tufts of short setae; lateral face with irregular row of tufts of short setae; mesial face with few tufts of short setae and single row of 5–7 small corneous spinules; ventral surface with 2 rows of tufts of long setae and row of 5–8 strong corneous spines increasing in size distally. Propodus moderately long, about 1.14 length of carpus; dorsal margin with double row of tufts of long setae and row of very low protuberances; lateral face with scattered tufts of moderately long setae and few spinules; mesial face with scattered tufts of long setae and few spinules; ventral face with two rows of tufts of long setae and two distinct corneous spines on distal margin. Carpus moderately long, 3/4 length of merus; dorsal surface with row of tufts of long setae and single distal marginal spine; lateral face with scattered tufts of long setae; mesial face with few tufts of setae; ventral surface with tufts of long setae on distal margin and midpoint. Merus laterally compressed; dorsal surface with row of low protuberances and single or double row of tufts of long setae; lateral and mesial surface with few short setae; ventral margin with strong spines and tufts of long setae. Ischium with long setae on dorsal margin; ventral surface with row of tufts of setae, terminal tuft composed of pronounced long setae. Coxa with short setae on ventrolateral margin; ventromesial margin with tufts of long setae and low protuberances.

Third pereopods approximately equaling length of second pair. Dactyl elongate, slender, equaling or slightly longer than propodus, slightly curved in lateral view, straight in dorsal view, terminating in strong corneous claw; dorsal surface with row of short setae; lateral face with few tufts of short setae; mesial face with 2 rows of 3–5 small corneous spines and few tufts of setae; ventral surface with row of 7–9 strong corneous spine increasing in size distally and with accompanying tufts of setae. Propodus long, about 1.20 length of carpus; dorsal surface with row of low protuberances and 2 rows of tufts of long setae; lateral and mesial face with scattered few setae; ventral surface with row of 4–6 small corneous spines and a double row of strong spines at distal end. Carpus 3/4 length of merus; dorsal surface with row of very low protuberances and tufts of long setae, distal margin with strong spine; lateral face with irregular rows of tufts of long setae; mesial and ventral faces with few tufts of long setae. Merus laterally compressed; dorsal surface with row of low protuberances and a double row of tufts of long setae; mesial and lateral faces with few tufts of setae; ventral margin with tufts of long setae. Ischium with long setae on ventral and dorsal margins; lateral and mesial faces unarmed. Coxa with tufts of long setae on ventromesial margin and distal end of ventral surface; few short setae on ventrolateral margin.

Anterior lobe of sternite of third pereopod subsemicircular, anterior margin with long setae and few spinules.

Telson with posterior lobes asymmetrical (left slightly larger), separated by median cleft; terminal margins with series of very tiny spines; lateral margins with three or more setae; anterior lobes each with long setae laterally and scattered setae of several lengths on surface.

Coloration. —In life: generally gray-green. Chelipeds pale blue-green with white bands on dactyl, fixed finger and proximal portion of merus; 2–3 blue-gray stripes on surface of palm. Ambulatory legs pale blue-green with dark brown stripes on dorsal, lateral and mesial surfaces of dactyl, propodus, and carpus and on dorsal and lateral surfaces of merus. Shield generally pale gray-green with scattered small dark blue-green patches. Ocular peduncles pale green with few white patches dorsally and mesially and dark gray patch at central portion.

In preservative (formalin): generally yellow-orange. Chelipeds with white closely-

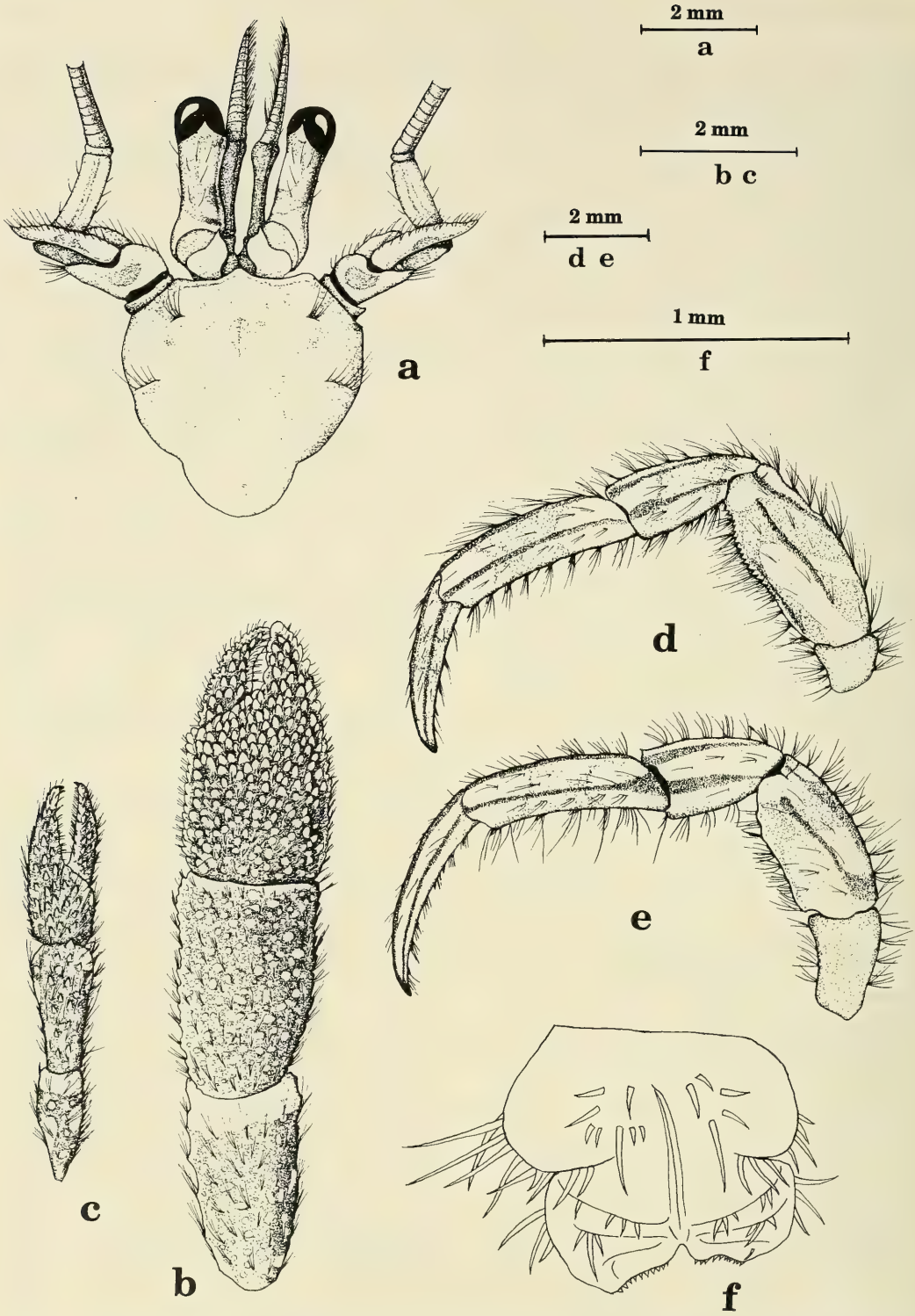


Fig. 1. *Pagurus insulae,* new species. Holotype, male (SL = 3.10 mm): a, shield and cephalic appendages; b, right cheliped, dorsal view; c, left cheliped, dorsal view; d, left second pereopod, lateral view; e, left third pereopod, lateral view; f, telson.

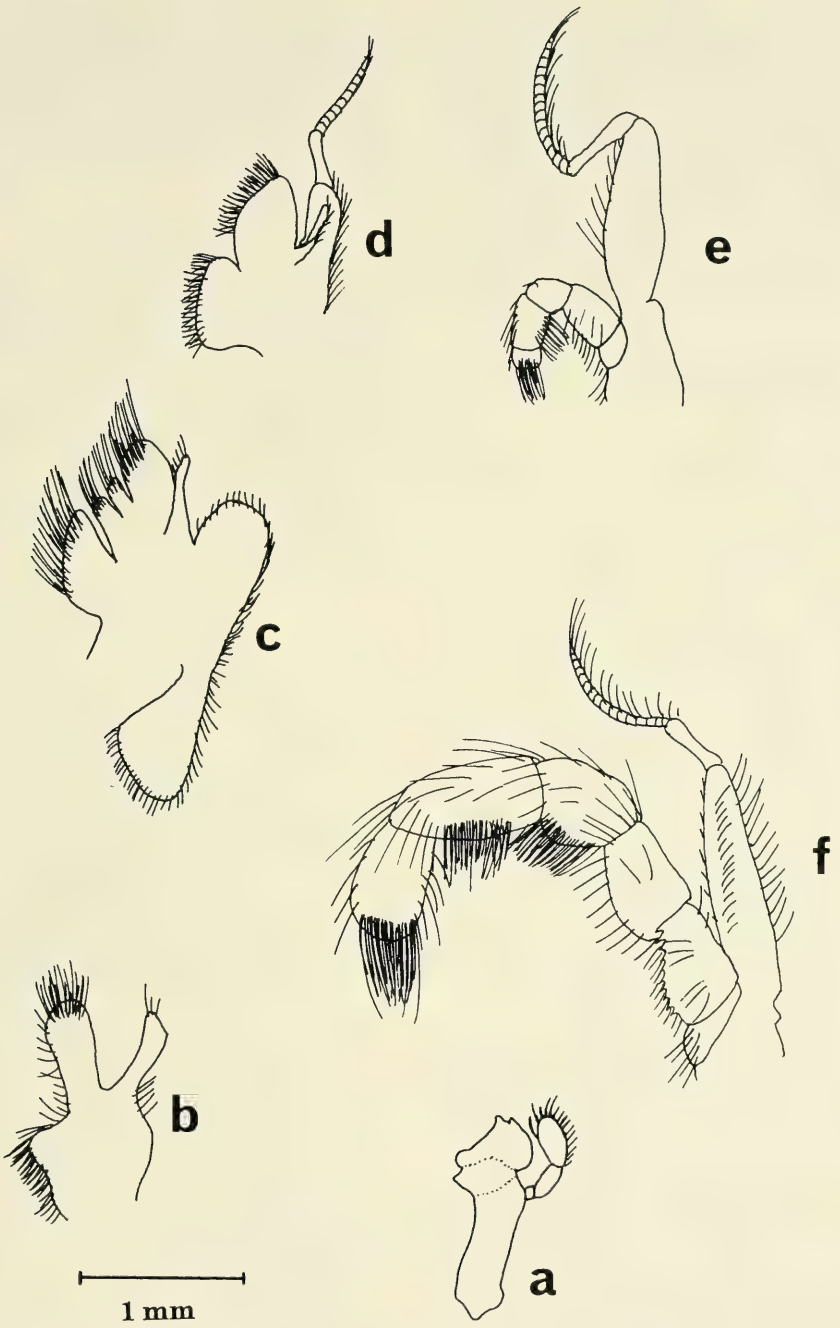


Fig. 2. *Pagurus insulae,* new species. Paratype, male. (SL = 3.00 mm). Mouthparts (right, internal view): a, mandible; b, maxillule; c, maxilla; d, first maxilliped; e, second maxilliped; f, third maxilliped.

spaced spines or tubercles on dactyl, palm and carpus; proximal portion of dorsal, mesial and lateral surfaces of merus with white bands. Ambulatory legs with red stripe on dorsal, lateral and mesial surfaces of dactyl, propodus, and carpus and on dorsal and lateral surfaces of merus. Shield whitish with small yellow patches. Ocular peduncles yellow-orange with few white patches dorsally and mesially.

Habitat.—The species was found in the intertidal zone of rocky shores and boulder beaches on Ogasawara.

Etymology.—This species is found in the oceanic island of Ogasawara and derives its name from the Latin "insula."

Remarks.—The new species shares many diagnostic characters with *Pagurus geminus* McLaughlin, 1976; however, there is no doubt that two species are distinct. The dactyls and propodi of the third pereopods of *P. geminus* each have a group of short spines on the ventrolateral face; the meri of the chelipeds each bear a blunt ventroproximal process. These spines and processes are absent in *P. insulae.* Color differences also readily distinguish the two species. The new species has dark brown stripes on the second and third pereopods, whereas *P. geminus* has broad white bands on the proximal and distal portions of the dactyls of the same (see Miyake 1982: pl. 44, fig. 5).

In having striped walking legs, *P. insulae* appears similar to *P. pilosipes* (Stimpson, 1858); however, the stripes are more reddish in the new species and the meri of its chelipeds lack the white distal band present in *P. pilosipes.* Examination of comparative material of *P. pilosipes* taken from Shiraiwa-zaki, Tomioka, the Amakusa Shimoshima Island, north western Kyushu, now in the collection of CBM, discloses that it is also readily distinguished from the new species by pronouncedly setose pereopods as suggested by the specific name. Also, the meri of the chelipeds of *P. pilosipes* bear two prominent ventroproximal processes, the propodus of the left third pereopod bears a group of small spines on the ventrolateral face, and the right cheliped bears 5–7 longitudinal rows of more prominent spines.

Distribution.—Okumura, Sakaiura, and Toufuiwa on Chichijima Island, the Ogasawara Islands.

Acknowledgments

I am indebted to Dr. K. Baba of Kumamoto University for his generous help, advice, and critical reading of the manuscript and to Dr. P. A. McLaughlin of Western Washington University for her critical reading of the manuscript. I also thank Mr. S. Nishihama of Amakusa Marine Biological Laboratory, Kyushu University for his aid in the field work.

Literature Cited

Habe, T., T. Akazawa, I. Fujiyama, Y. Kuwano, H. Morioka, T. Nakaike, M. Takeda, M. Watanabe, & B. Yamaguchi. 1978. The natural history research of the Izu-Mariana Arc.—Bulletin of the National Science Museum, Tokyo 11:1–10.

Hirota, S. 1894. Animals of Ogasawara.—Zoological Magazine, Tokyo 6:195–206, 233–247.

Imajima, M. 1970. Marine organisms. Pp. 179–196 *in* N. Tsuyama & S. Senkai, eds., The Nature of Ogasawara. Hirokawa-shoten, Tokyo, 271 pp.

McLaughlin, P. A. 1974. The hermit crabs (Crustacea Decapoda, Paguridea) of northwestern North America.—Zoologische Verhandelingen, Leiden 130:1–396, pl. 1.

——— 1976. A new Japanese hermit crab (Decapoda, Paguridae) resembling *Pagurus samuelis* (Stimpson).—Crustaceana 30:13–26.

Melin, G. 1939. Paguriden und Galatheiden von Prof. Dr. Sixten Bocks Expedition nach den Bonin-Inseln 1914.—Kungl Svenska Vetenskaps Akademitens Handlingar, Stockholm, serien 3, 18: 1–119.

Miyake, S. 1982. Japanese crustacean decapods and stomatopods in color. I. Macrura, Anomura and Stomatopoda. Hoikusha, Osaka, 261 pp. + 56 pls.

Ooishi, S. 1970. Marine invertebrate fauna of the Ogasawara and Volcano Islands collected by S. Ooishi, Y. Tomida, K. Izawa and S. Manabe. Pp. 75–104 + pls. 1–25, *in* Report on the marine biological Expedition to the Ogasawara (Bonin) Islands, 1968, 104 pp. + 25 pls.

Shigei, M. 1970. Marine invertebrate fauna of the

Bonin Islands. Pp. 45–66 *in* The nature of the Bonin and the Volcano Islands. Higher Education and Science Bureau, Ministry of Education and Cultural Properties Protection Division, Agency for Cultural Affairs, Japan, 91 pp.

Stimpson, W. 1858. Prodromus descritptionis animalium evertebratorum, quae in expeditione ad Oceanum Pacificum.—Proceedings of the Academy of Natural Sciences of Philadelphia 10:31–40.

———. 1907. Reports on the Crustacea (Brachyura and Anomura) collected by the North Exploring Expedition, 1853–1856.—Smithsonian Miscellaneous Collection 49:1–240, pls. 1–26.

Sugano, T. 1974. Report on the marine animals. Pp. 22–44 *in* The Investigation of fauna and flora of the Ogasawara Islands. Department of Biology, Faculty of Science, Tokyo Metropolitan University, 86 pp.

Takeda, M. 1981. A new hermit crab of the genus *Porcellanopagurus* from the Ogasawara Islands.—Bulletin of the Biogeographical Society of Japan 36:8–13.

Terao, A. 1913. A catalogue of hermit-crabs found in Japan, with descriptions of four new species.—Annotationes Zoologicae Japanenses 8: 355–391.

Yoshiwara, S. 1901. Animals of Ogasawara.—Zoological Magazine, Tokyo 13:309–316.

Natural History Museum and Institute, Chiba. 955-2, Aoba-cho, Chiba-shi, 280, Japan.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 800–811

A NEW GENERIC ASSIGNMENT FOR A SOUTH AMERICAN CRAYFISH (DECAPODA: PARASTACIDAE) WITH REVISED DIAGNOSES OF THE SOUTH AMERICAN GENERA AND COMMENTS ON THE PARASTACID MANDIBLE

Horton H. Hobbs, Jr.

Abstract.—A new monotypic genus, *Virilastacus,* is proposed to receive the disjunct species *Parastacus araucanius* Faxon (1914), which in 1971 was assigned by Riek to the genus *Samastacus.* For comparative purposes, illustrations of the salient features of this crayfish and of the sole member of *Samastacus, S. spinifrons* (Philippi, 1882), are provided, as is a redescription of *Virilastacus araucanius.* Similarities and differences between them and two sympatric members of the genus *Parastacus* are summarized. Diagnoses of the three genera of South American Parastacidae are provided along with comments on mandibular features.

A draft of this manuscript was completed in 1987, and copies were circulated among students of the Parastacidae (see "Acknowledgments") for their perusal. Before I received their comments, I learned from Dr. Ludwig Buckup that he had just submitted a manuscript treating the South American crayfishes on the Pacific versant. Moreover, he stated that he had found additional specimens of *Samastacus araucanius* (Faxon, 1914) in the Museum of Zoology, Hamburg, Germany, that were being described. Without notifying Dr. Buckup of my having duplicated, at least in part, his effort, my manuscript was filed awaiting the appearance of his publication. A recent letter from him revealed that the manuscript is still in press.

In the meantime, I found that I had overlooked an abstract published by Jara (1983) announcing the discovery of a second locality for this crayfish and a suggestion that it should perhaps be assigned to a new genus. The latter was amplified by Rudolph & Rivas (1988), who also provided an illustration of the phallic papillae and coxae of the fourth and fifth pereiopods. C. G. Jara, who has donated two specimens of this species to the Smithsonian, recently read this manuscript and has encouraged me to offer it for publication. While the common possession of certain features suggests closer affinities between *Samastacus araucanius* and *S. spinifrons* than those binding either to the species currently assigned to the genus *Parastacus,* there are so many distinctive features (see "Diagnosis," Table 2, and illustrations) exhibited by these two species now assigned to *Samastacus* that they must have shared only a very remote common ancestry. In recognition of this opinion, which is shared by Jara (1983) and Rudolph & Rivas (1988), I propose that Faxon's *Parastacus araucanius,* redescribed and illustrated herein, be assigned to a new, monotypic genus. Included also are modifications of the diagnoses of the genera *Parastacus* and *Samastacus* presented by Hobbs (1974).

Parastacus Huxley, 1879

Parastacus Huxley, 1879:759, 771 [Type species, by subsequent designation (Faxon, 1898:683): *Astacus pilimanus* von Martens, 1869:15. Gender: masculine.]

Diagnosis.—Carapace lacking spines and tubercles and with or without postorbital ridges; anterolateral part of branchiocardiac groove often hardly distinguishable because of closely approximating deeply impressed cervical groove, 2 usually merging dorsolaterally; viewed dorsally, cervical groove somewhat V-shaped except in *P. laevigatus*; postorbital ridge ranging from well developed to virtually obsolete. Abdomen without tubercles or spines; pleuron of first abdominal segment distinct and partly overlapped by that of second. Telson entirely, sometimes weakly, calcified; without transverse suture but with dorsomedian longitudinal sulcus (sometimes rudimentary). Third maxilliped with mesial half of ventral surface of ischium bearing setiferous punctations; exopodite reaching, or slightly overreaching, basal part of merus. Caudal molar process of mandible mostly bicuspide, but tricuspide in *P. saffordi* and quadricuspide in *P. varicosus* in which nodular cusp located on proximal side of cuspal triangle. Chela with ventrolateral margin smooth or bearing small tubercles; when upper surface of carpus of cheliped held in horizontal plane, dactyl moving subvertically; carpus with or without spiniform tubercles. Male genitalia consisting of fixed, slightly elevated ventromesial ridge bearing noncalcified phallic papilla; male cuticle partition (see Morgan, 1986) present; all members with at least rudiments of male and female genital apertures. Branchial count 20 + epr + r, or 20 + ep + r (podobranchs on segments VIII–XIII; anterior arthrobranchs on VIII–XIII; posterior arthrobranchs on IX–XIII, that on 13 rudimentary; pleurobranchs on XI–XIV; and epipodite on VII bearing few branchial filaments). Lateral processess of sternite XIV contiguous along at least part, often much, of their length, separated by short or long fissure.

Species.—*Parastacus brasiliensis* (von Martens, 1869:16), *P. defossus* Faxon (1898: 686), *P. laevigatus* Buckup & Rossi (1980: 677), *P. nicoleti* (Philippi, 1882:624), *P. pilimanus* (von Martens, 1869:15), *P. pugnax* (Poeppig, 1835:314), *P. saffordi* Faxon (1898:683), and *P. varicosus* Faxon (1898: 685) (see Hobbs 1989, for most recent summary of synonymies and ranges).

Samastacus Riek, 1971

Samastacus Riek, 1971:134 [Type species, by original designation, *Astacus spinifrons* Philippi, 1882:687. Gender: masculine].—Hobbs, 1974:26.

Diagnosis.—Carapace punctate or smooth; anterolateral part of branchiocardiac groove extending subparallel to cervical groove, 2 merging laterally; viewed dorsally, cervical groove broadly U-shaped; postorbital ridge well developed, terminating anteriorly in spine or tubercle. Abdomen without spines or tubercles; pleuron of first abdominal segment distinct and partly overlapped by that of second. Telson entirely calcified, without transverse suture and dorsomedian longitudinal sulcus. Third maxilliped with setiferous punctations over entire ventral surface; exopodite reaching, or slightly overreaching distal extremity of ischium. Caudal molar process of mandible quadricuspide with nodular cusp on distal side of cuspal triangle. Chela with ventrolateral margin smooth; when upper surface of carpus of cheliped held in horizontal plane, dactyl moving subhorizontally; carpus without enlarged spiniform tubercles mesially and ventrally. Male genitalia consisting of articulated, slender, tubular, calcified projections, which shorter than length of widely separated coxae; latter with male cuticle partition; individuals never with even rudiments of both male and female genital apertures. Branchial count: 20 + ep + r. Sternite XIII with median, caudally pro-

jecting, digitiform element. Lateral processes of sternite XIV widely separated.

Species.—*Samastacus spinifrons* (Philippi, 1882:627). See Figs. 1 and 3g.

Virilastacus, new genus

Parastacus.—Faxon, 1914:353 [in part].
Samastacus Riek, 1971:135 [in part].

Diagnosis.—Carapace lacking spines, tubercles, and postorbital ridges; anterolateral part of branchiocardiac groove distinctly separated from the subparallel to cervical groove along upper third of height of carapace; viewed dorsally, cervical groove weakly V-shaped and not deeply impressed. Abdomen lacking spines and tubercles; pleuron of first abdominal segment distinct and partly overlapped by that of second. Telson with no trace of transverse suture and entirely calcified; posterior half with dorsomedian longitudinal sulcus. Ventral surface of ischium of third maxilliped with median longitudinal band of tubercles and mesial half bearing tufts of stiff setae; distolateral extremity of podomere rounded, not produced; merus without spines and tubercles; exopod reaching distal extremity of merus. Caudal molar process of mandible quadricuspide; nodular cusp situated on proximal side of cuspal triangle. Chela with palm almost entirely tuberculate, lacking spines or large tubercles; ventrolateral margin tuberculate to weakly subserrate; when upper surface of carpus held in horizontal plane, dactyl moving obliquely, neither subvertically nor subhorizontally; carpus of cheliped lacking enlarged tubercles mesially and ventrally. Male genitalia consisting of articulated, slender, tubular, semi-rigid phallic papilla which longer than length of, and extending anteriorly from, narrowly separated coxae which lacking male cuticle partition (see Morgan, 1986:7); never with both male and female genital apertures. Sternite XIII with cephalically cleft median plate posteriorly. Lateral processes of sternite XIV separated in caudal aspect by distinct vertical fissure.

Type species.—*Parastacus araucanius* Faxon, 1914:353.

Gender.—Masculine.

Etymology.—L. *virilis* = manly; so-named because of the comparatively long phallic papillae.

Virilastacus araucanius (Faxon, 1914), new combination
Figures 2, 3a, j, l, m

Parastacus araucanius Faxon, 1914:353–354, 406, plate 4 [Holotype: Museum of Comparative Zoology 7355 (♂). Type locality: Corral, Chile].—Van Straelen, 1942:9.—Holthuis, 1952:84.—Bahamonde, 1958:186.—Bahamonde & López, 1963:126, 127.—Castro, 1966:11, 17.—Riek, 1971:135.—Jara, 1983:R-163.
Samastacus araucanius.—Riek, 1971: 135.—Manning & Hobbs, 1977:159.—Buckup & Rossi, 1986:54.—Rudolph & Rivas, 1988:73–78. fig. 1.—Hobbs, 1989: 80, fig. 127.

Description of holotype.—Rostrum (Fig. 2, b, d, i) short, constituting 11.2% of carapace length, with smooth, weakly convergent lateral carinae; lateral margin (= subrostral ridge) evident in dorsal view to near tip of rostrum; dorsal surface excavate anteriorly grading to subplane posteriorly. Postorbital ridges obsolete. Suborbital angle prominent although rounded apically. Mandibular arc conspicuously elevated, but lacking tubercles along ventral margin. Branchiostegites punctate dorsally, granulate ventrally; cervical and branchiostegal spines absent; anteroventral branchiostegal region studded with very small squamous tubercles. Areola (Fig. 2f, i) 1.9 times as long as wide, constituting 32.0% of carapace length and 35.8% of postorbital carapace length.

Basal podomere of antennular peduncle with strong median spine slightly proximal

Fig. 1. *Samastacus spinifrons* from Los Cuartos, Bío Bío Province, Chile. a, Lateral view of body with ambulatory appendages removed; b, Dorsal view of antennal scale and adjacent structures; c, Epistome and base of antenna; d, Lateral view of cephalic region; e, Dorsal view of distal podomeres of cheliped; f, Dorsolateral view of cardiac and gastric regions of carapace; g, Ventral view of ischium, merus, and exopod of right third maxilliped; h, Dorsal view of telson; i, Dorsal view of carapace and chelipeds; j, Caudal view of basal podomeres of fifth pereiopods and adjacent structures; k, Ventral view of sternal region.

to midlength. Antennal peduncle with obtuse submedian tubercle and weak lateral elevation on distal margin of coxa (Fig. 2c), otherwise without spines or tubercles. Antennal scale (Fig. 2b) broad and short, widest distal to midlength, and with single distolateral spine reaching base of ultimate podomere of antennular peduncle; flagel-

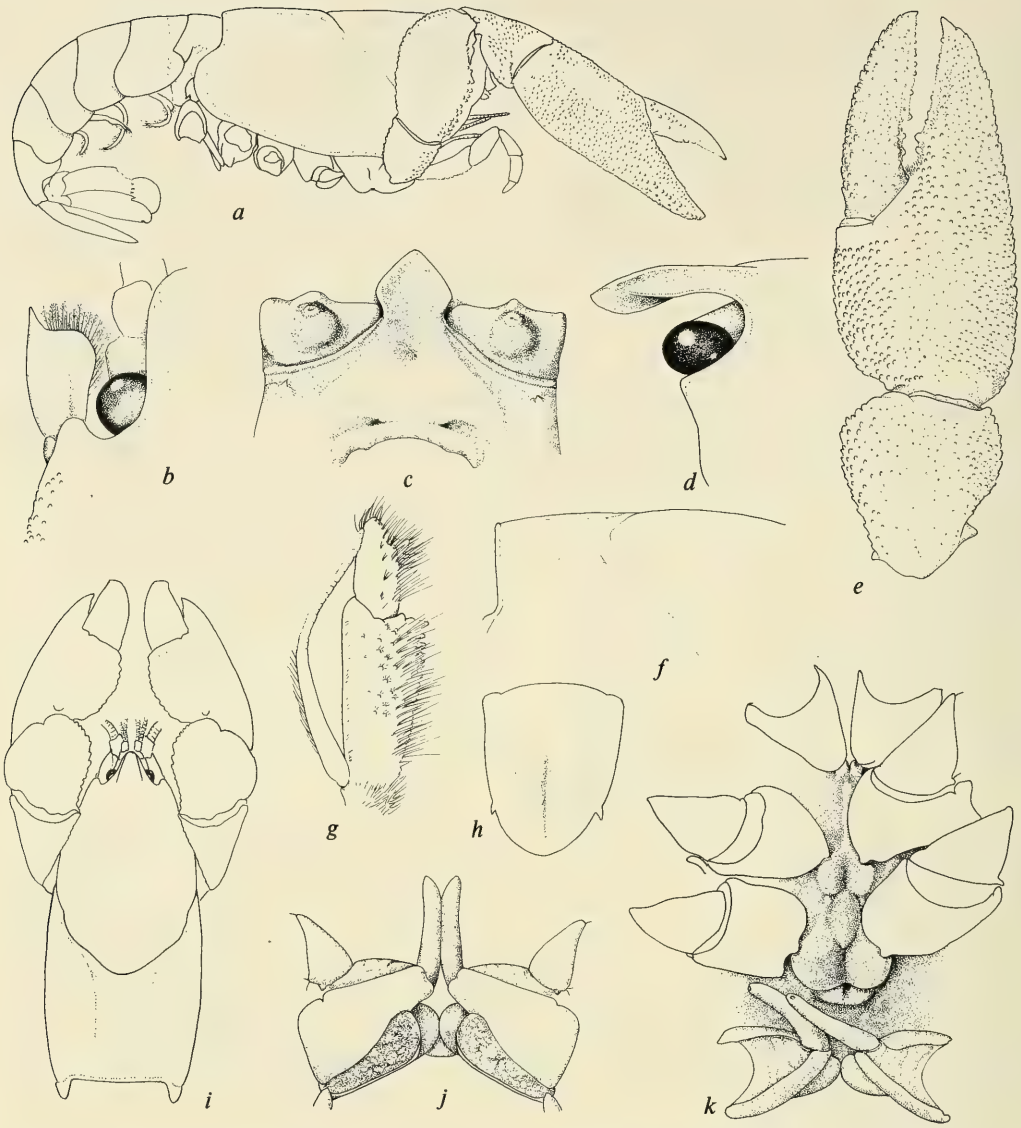


Fig. 2. Holotype of *Virilastacus araucanius*. a, Lateral view of body with ambulatory appendages removed; b, Dorsal view of antennal scale and adjacent structures; c, Epistome and base of antenna; d, Lateral view of cephalic region; e, Dorsal view of distal podomeres of cheliped; f, Dorsolateral view of cardiac and gastric regions of carapace; g, Ventral view of ischium, merus, and exopod of right third maxilliped; h, Dorsal view of telson; i, Dorsal view of carapace and chelipeds (left cheliped in specimen regenerated, mirrored image of right one depicted here); j, Caudal view of basal podomeres of fifth pereiopods and adjacent structures; k, Ventral view of sternal region.

lum of both antennae broken. Mandible with both cephalodistal and proximocephalic cusps sclerotized and contiguous to cephalic molar process, and smaller sclerotized distoproximal cusp somewhat removed from them; arrangement resembling that illustrated for *Euastacus yarransis* (McCoy, 1888:225) by Hobbs, 1987: fig. 3a. Ischium of third maxilliped (Fig. 2g) not produced distolaterally; clusters of setae on mesial

Table 1.—Measurements (in mm) of *Virilastacus arauncanius*.

Structure	Holotype ♂	Valdivia		Hualqui	
		♂	♀	?*	♂*
Carapace					
Length	18.8	24.0	20.4	26.0	19.0
Postorbital length	16.8	**21.5	18.0	?	?
Areola					
Length	6.0	**7.7	6.8	8.4?	7.8
Width	3.2	?	3.0	4.0	4.3
Chela					
Length	14.8	23.6	15.6	26.4	23.7
Palm width	7.1	11.9	8.7	12.8	12.8

* Data from Rudolph & Rivas (1988).
** Extrapolated from proportions in female; see text.

sector stiff; merus without spines and tubercles mesially and laterally.

Epistome (Fig. 2c) with small cluster of tubercles anterolaterally, one of dextral members spiniform, and submedian fovea posterior to subtriangular anteromedian lobe, latter with smooth margins.

Keel of sternite XIII (Fig. 2k) with cephalically cleft median plate posteriorly [perhaps homologous to bullar lobes in some members of *Astacoides* (see Hobbs 1987:fig. 5)]. Median keel of sternite XII not inflated, that of XIII strongly so. Lateral processes of sternite XI small and directed ventrally, those of sternite XII disposed at approximately 90° to one another, and those of sternite XIII, at about 12°. Vertical arms of paired sternopleural bars of segment XIV widely separated, clearly exposing lateral processes separated by median fissure; bullar lobes not differentiated.

Cheliped (Fig. 2a, e, i) with mesial border of ischium studded with small tubercles. Ventral surface of merus with 2 lateral, sublinear, longitudinal series of about 8 tubercles each (others flanking rows), and single mesial row of about 12 smaller tubercles; dorsal surface also bearing distally-broadening band of small tubercles, none conspicuously larger than others nearby, and none spiniform; dorsodistal margin smooth, not crenulate. Carpus with mesiodistal subcristiform row of five or six small tubercles, podomere mostly tuberculate, largest tubercles along ventral part of distal margin; median depression on dorsal surface very shallow. Propodus width 48% of length, tubercles on lateral surface extending onto finger where dividing into 2 rows separated by series of conspicuous punctations; mesial surface of palm studded with tubercles. Opposable margin of fixed finger with single row of minute denticles flanked proximodorsally by 2 rather conspicuous tubercles followed by broken series of 6 smaller tubercles more distally; ventral flank with row of 6 small tubercles along distal half of finger (not visible in Fig. 2e). Dactyl tuberculate mesially; opposable margin with single row of minute denticles flanked dorsally by row of 10 small tubercles and single larger tubercle ventrally, latter occupying gap between second and third tubercles of dorsal row. Ventromesial surfaces of both fingers punctate with moderate clusters of setae basally.

Pleura of abdominal segments as illustrated (Fig. 2a), lacking tubercles and spines. Telson (Fig. 2h) heavily calcified, setose, punctate dorsally with caudomedian longitudinal sulcus and single pair of fixed marginal spines; no trace of transverse suture evident. Proximal podomere of uropod lacking spines and tubercles; mesial ramus

with well defined median carina bearing premarginal distal spine, and lateral margin also with single fixed spine. Lateral ramus with median keel and row or 10 spines on proximal side of diaeresis. Lateral angle of anterior section (probably injured in earlier instar) lacking spines on left member, right with 1 fixed marginal spine and broken articulated one and fixed one mesial to it.

Phallic papillae (Fig. 2j, k) tubular and long, extending anteriorly from ventral anteromesial angle of coxa, and reaching distinctly anterior to ventral articular condyle of coxa of fourth pereiopod when fifth pereiopods pressed anteriorly.

Male from Valdivia.—(The carapace of this specimen is crushed and the entire dorsal part of the thoracic region is missing. The carapace dimensions cited are extrapolated on the basis of the length of the cephalic region, the dorsal part of which is entire, in comparison with that of the female from the same locality.) Differing from holotype in following respects: Antennal flagellum reaching second abdominal tergum. Mandible (Fig. 3a) essentially similar but 1 of 4 cusps on caudal molar process not observed in holotype. Epistome with anteromedian lobe more nearly sagittiform than triangular; plumose setae, made more conspicuous by adhering clay particles, on plane and marginal surfaces. Lateral processes of sternites XII and XIII splayed at angles of approximately 80° and 90° respectively. Cheliped with only 5 tubercles in more mesial of two lateral rows on ventral surface of merus; carpus more weakly tuberculate and many replaced by punctations, especially dorsolaterally; propodus width 50% of length. Chela (Fig. 3m) with punctations on lateral surface of fixed finger inconspicuous; opposable margin of fixed finger with small tubercle at base followed by massive, bifid one, and row of small tubercles extending distally from base of latter almost to corneous tip of finger; distal 4 tubercles of row flanked ventrally by row of recessed minute denticles and 4 more ventrally situated tubercles; opposable margin of dactyl with 2 tubercles in proximal concavity opposing bifid tubercle on fixed finger, and row of 10 tubercles continuing distally from concavity almost to corneous tip of finger. Undivided telson with pair of weak marginal tubercles and median longitudinal groove (Fig. 3l); lateral margin of uropod with 2 lateral spines and 9 or 10 in row on proximal flank of diaeresis.

Female from Valdivia.—Differing from holotype in following respects: Areola 2.3 times as long as broad, constituting 33% of carapace length, 38% of postorbital carapace length. Antennular peduncle lacking spine on basal podomere. Lateral processes of sternites XII and XIII not so strongly splayed. Width of propodus of right chela 55.8% of length. Tubercles on lateral surface of chela not so clearly arranged in rows and setiferous punctations not conspicuous. Opposable margin of propodus like that of Valdivia male except 6 tubercles present in more ventral distal row and setal cluster present proximal to massive tubercle; opposable margin of dactyl as in Valdivia male. Left chela much smaller than right, probably regenerated (?). Lateral ramus of uropod also like that of latter except 12 spines present on proximal flank of diaeresis.

Ovate oviducal apertures unremarkable.

Material examined.—Holotypic male, and a male and female from the Botanical Garden, Universidad Austral de Chile, Valdivia, collected 1 Dec 1983 by C. G. Jara. (See Table 1 for measurements.)

Observations on the mandible of South American parastacids.—The following observations are based on limited material and whether or not these remarks and accompanying illustrations are typical of the species must be confirmed. At least one mandible of each of the South American species, except those of *Parastacus laevigatus,* have been examined and are illustrated in Figure 3. The incisor lobe varies little, and the number of denticles ranges from 9 to 10; in all of them, except *P. nicoleti,* the antipen-

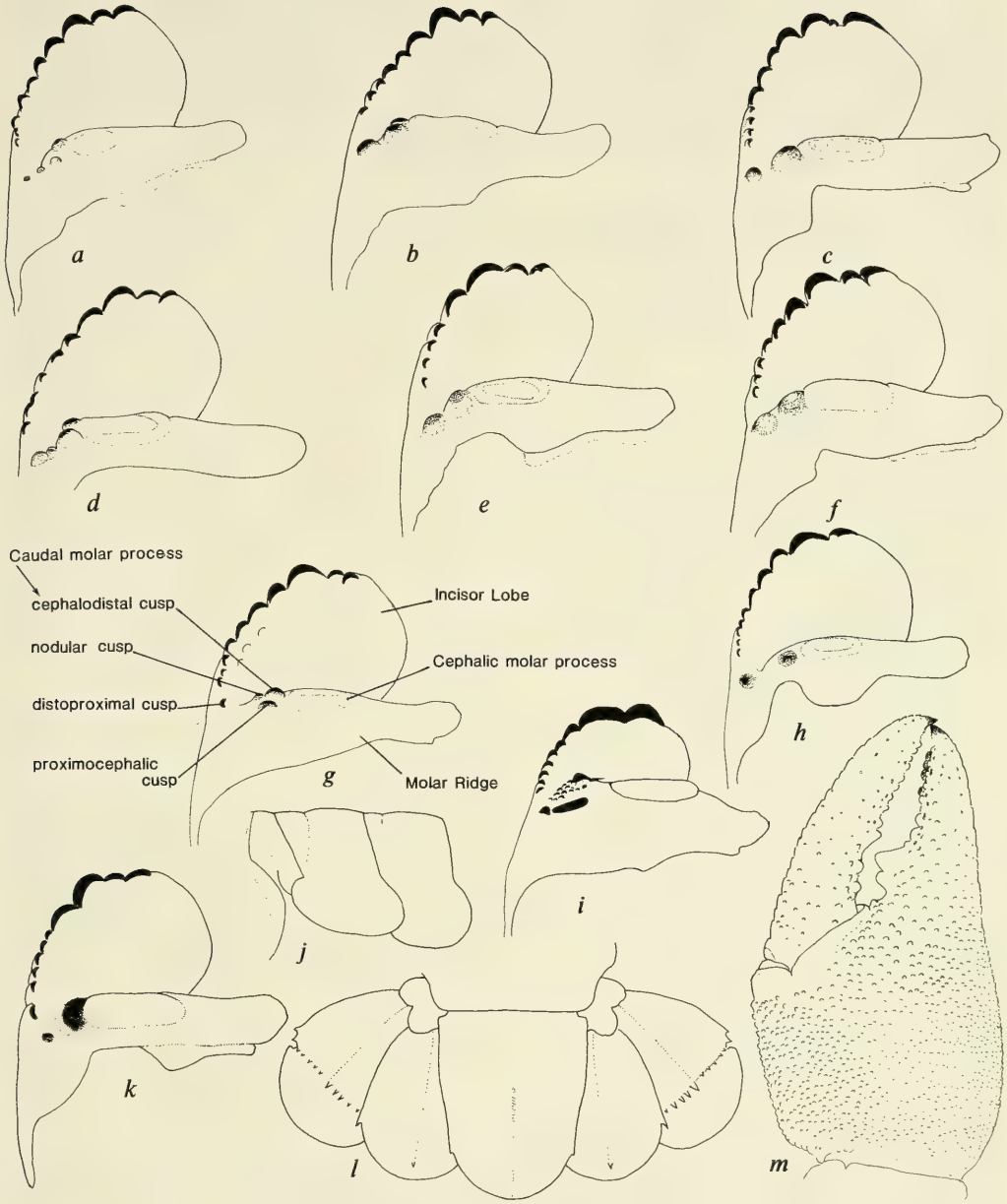


Fig. 3. Parastacid mandibles and features of male *Virilastacus araucanius* from Valdivia, Chile. (a–i, k, Caudal view of mandibles; j, Lateral view of anterior abdominal segments; l, Dorsal view of telson and uropods; m, Dorsal view of chela.) a, j, l, m, *Virilastacus araucanius*; b, *Parastacus saffordi*; c, *P. pugnax*; d, *P. varicosus*; e, *P. pilimanus*; f, *P. defossus*; g, *Samastacus spinifrons*; h, *Parastacus nicoleti*; i, *Astacoides granulimanus* (from Madagascar); k, *Parastacus brasiliensis.*

ultimate tooth is the largest. In the latter the penultimate is largest, as it is in all members of the genus *Astacoides* and in *Euastacus yarraensis* (McCoy, 1888) and *Astacopsis franklinii* Huxley (1879) (see Hobbs 1987: 11).

In all of the South American species the mandibles of which have been examined, the cephalic and caudal molar processes are, or are almost, contiguous. Only the caudal molar process exhibits possible noteworthy differences. In his study of the mandibles of the crayfishes of Madagascar, Hobbs (1987) employed the terminology proposed by Bouchard (1977) in his pioneering survey of mandibular features of holarctic crayfishes, introducing only one new feature that was termed the "nodular cluster" (referring to a group of cusps not known to exist in the caudal molar process of members of the Astacidae and Cambaridae). In attempting to homologize the mandibular features of the South American crayfishes with those of the holartic crayfishes and those of Madagascar, problems were encountered in attempting to identify the denticles in those that exhibited a variable quadricuspide caudal molar process and those that posessed a bicuspide one. A solution, seemingly reasonable to me, was reached in following the basic triangular pattern recognized by Bouchard in the Holarctic crayfishes: the side marked by the distoproximal and proximocephalic cusps as the proximal side of the triangle, and that between the distoproximal cusp and cephalodistal cusp, the distal. If the fourth cusp in the quadricuspide process is interpreted as representing a member of the "nodular cluster" of *Astacoides* than the "extra cusp" in *Virilastacus araucanius* and *Parastacus varicosus,* is a nodular cusp aligned on the proximal side of the cuspal triangle; in *Samastacus spinifrons* and *Astacopsis franklinii* the nodular cusp (perhaps another member of the nodular cluster) is aligned on the distal side of the triangle. Whether or not the nodular cusps occupying different sides of the cuspal triangle are homologous or represent retentions of different cusps in the nodular cluster remains to be demonstrated.

Perhaps speculations on the probable evolutionary sequence in the evolution of the cuspal triangle of the caudal molar process are premature, but I suggest that on the assumption that elements are more readily lost than gained, the most primitive condition of the caudal molar process occurs in the more generalized members of *Astacoides* (Fig. 3i) in which a cluster of nodular cusps lies within and on the distal side of the cuspal triangle. With the loss of all except two members of the nodular cluster that lie on the distal side of the triangle the condition found in *Astacopsis crosnieri* (see Fig. 3c in Hobbs 1987) is reached, and with the loss of one of these nodular cusps the cuspal composition of the caudal molar process of *Astacopsis franklinii* (see Fig. 3b in Hobbs 1987) and *Samastacus spinifrons* (Fig. 3g herein) has been attained. With the cephalic migration of the single nodular cusp to the proximal side of the cuspal triangle the pattern exemplified by *Virilastacus araucanius* and *Parastacus varicosus* has arisen, and with the loss of all of the nodular cusps the simple triangular caudal molar process exhibited by *Parastacus saffordi* and *Euastacus yarraensis* came into existence. As for the bicuspid caudal molar process, I suggest that a fusion of the two lateral elements of the cuspal triangle (cephalodistal and proximocephalic cusps) would account for the more lateral cusp of the bicuspid mandible characteristic of most members of the genus *Parastacus.* The possibility of the occurrence of such a fusion is perhaps strengthened by the large size of the lateral cusp in *P. brasiliensis* (Fig. 3k).

Remarks.—Rudolph & Rivas (1988:Table 1), in their study of *Virilastacus araucanius* presented measurements for what they termed the "Quela mayor" and the "Quela menor." This suggests to me that they consider the chelae of this crayfish to be dimorphic, as they are in at least some lobsters in which there is a "crushing-" and a "cutting-claw." Although I may be in error

Table 2.—Comparison of features of representatives of three South American crayfish genera.

Feature	*V. araucanius*	*S. spinifrons*	*P. pugnax*	*P. nicoleti*
Telson	calcified; with median sulcus & marginal spines	partly calcified, flexible; no median sulcus; with marginal spines	calcified; with median sulcus & marginal spines	calcified; with median sulcus; no marginal spines
Rostrum	reduced	long	reduced	reduced
Postorbital ridges	absent	well developed	present	absent
Cervical groove	V-shaped	U-shaped	V-shaped	V-shaped
Branchiocardiac groove	not joining cervical	joining cervical	joining cervical	joining cervical
Eyes	reduced	large	small	small
Mandible*	quadricuspide, nodular cusp on proximal side of triangle	quadricuspide, nodular cusp on distal side of triangle	bicuspide	bicuspide
Sternite XIII	with posteromedian plate	with long, digitiform projection	without caudal prominence	without caudal prominence
Sternite XIV	with deep median fissure	lacking median fissure	with deep median fissure	with deep median fissure
Mxp. III	sparsely setose, with band of tubercles	densely setose, no tubercles	sparsely setose, no tubercles	sparsely setose, no tubercles
Coxae XIV	close together, width about 2 × height	far apart, width < 2 × height	close together, width much < 2 × height	close together, width coxae much < 2 × height
Phallus	long	short	tuberculiform	tuberculiform
♂ cuticle partition	absent	present	present	present
Genital apertures	male or female	male or female	male and female	male and female
Chela: lateral margin dactyl	with tubercles row of mesial tubercles motion subhorizontal	without tubercles few mesial tubercles motion subhorizontal	few tubercles no mesial tubercles motion subvertical	2 rows of tubercles few mesial tubercles motion subvertical
Branchiae	20 + ep + r	20 + ep + r	20 + epr + r	20 + epr + r(?)
Habitat	burrows	open water	burrows	burrows

* Triangle of caudal molar process.

in doubting that such a dimorphic state exists in this crayfish, I am inclined toward the same opinion I expressed (Hobbs 1987: 8) after examining as many specimens of *Astacoides* as were available and concluded that the smaller cheliped in all members of that genus are ones that had been lost and regenerated.

Unfortunately, I have been able to examine only three specimens of *V. araucanius*: the holotype possesses chelae of unequal size, the left, interpreted by me to be a regenerate, much smaller than the right; the Valdivia male has only one chela (Fig. 3l); and the female aso has two chelipeds, but the smaller of the two has, in my opinion, all the characteristics of a regenerated appendage. To my knowledge, the existence of dimorphic chelipeds in which neither appendage has been regenerated has not been established for any astacoidean.

Although probably as closely allied to *Samastacus spinifrons* (Philippi, 1882) as to any other extant crayfish, among the many

features that serve to distingish *V. araucanius* from it are those listed in Table 2. That little reduction in the abdomen of the latter exists is rather surprising in view of the presence of other features that are frequently, if not usually, associated with a largely fossorial existence. Some, and perhaps even most, of the differences listed between them, as well as between them and two sympatric members of the genus *Parastacus,* conceivably might be either primarily or secondarily correlated with the habitats occupied by them: *S. spinifrons* principally occupying open water, and *V. araucanius* largely confined to burrows. But the differences in the phallic papillae and the associated features of the coxae bearing them, as well as the median structures of sternite XIII and perhaps those noted in the telson, were probably little influenced in their divergence by environmental factors.

Because the retention of these crayfishes in a common genus suggests to me a closer affinity between them than is warranted on the basis of our current understanding of the South American parastacids, the assignment of Faxon's *Parastacus araucanius* to a monotypic genus seems preferable to its current taxonomic position.

Acknowledgments

I am grateful to Herbert W. Levi of the Museum of Zoology, Harvard University, for lending me the unique type of the species treated here. For their comments on the manuscript, thanks are extended to L. B. Holthuis, of the Rijksmuseum van Natuurlijke Historie, G. J. Morgan, of the Western Australian Museum, P. Horwitz and A. M. M. Richardson, of the University of Tasmania, C. G. Jara of Universidad Austral de Chile, and to my Smithsonian colleague B. F. Kensley.

Literature Cited

Bahamonde, N. N. 1958. Sobre la validez taxonómica de *Parastacus nicoleti* (Philippi), 1882, y algunos aspectos de su biología.—Investigaciones Zoológicas Chilenas 4:183–198, 1B figures.

———, & M. T. López B. 1963. Decápodos de aguas continentales en Chile.—Investigaciones Zoológicas Chilenas 10:123–149.

Bouchard, R. W. 1977. Morphology of the mandible in holarctic crayfishes (Decapoda: Astacidae and Cambaridae): ecological and phylogenetic implications. Pp. 425–452 *in* Ossi V. Lindqvist, ed., Freshwater Crayfish 3. Papers from the Third International Symposium on Freshwater Crayfish. Kuopio, Finland: University of Kuopio. (Reprinted 1980 by International Association of Astacology, University of Kuopio, Finland.)

Buckup, L., & A. Rossi. 1980. O genero *Parastacus* no Brasil (Crustacea, Decapoda, Parastacidae).—Revista Brasilerira Biologia 40(4):663–681.

———, & ———. 1986. Os Parastacidae do espaço meridional Andino (Crustacea, Astacidea). Page 54 *in* XIII Congreso Brasileiro de Zoologia, Resumos, 2–7 Febreiro 1986. Cuiaba, Mato Grosso, Brasil.

Castro, C. 1966. El camarón de Río del Norte *Cryphiops caementarius* (Molina).—Estudios Oceanológicos (Universidad de Chile) 2:11–19, pls. 1–3.

Faxon, W. 1898. Observations on the Astacidae in the United States National Museum and in the Museum of Comparative Zoology, with descriptions of new species.—Proceedings of the United States National Museum 20(1136):643–694.

———. 1914. Notes on the crayfishes in the United States National Museum and the Museum of Comparative Zoology with descriptions of new species and subspecies to which is appended a catalogue of the known species and subspecies.—Memoirs of the Museum of Comparative Zoölogy at Harvard College 40(8):351–427, 13 pls.

Hobbs, H. H., Jr. 1974. Synopsis of the families and genera of crayfishes (Crustacea: Decapoda).—Smithsonian Contributions to Zoology 164:iii + 32 pp., 27 figs.

———. 1987. A review of the crayfish genus *Astacoides* (Decapoda: Parastacidae).—Smithsonian Contributions to Zoology 443:iii + 50 pp., 23 figs.

———. 1989. An illustrated checklist of the American crayfishes (Decapoda: Astacidae, Cambaridae, and Parastacidae).—Smithsonian Contributions to Zoology 480:iii + 236 pp., 379 figs.

Holthuis, L. B. 1952. The Crustacea Decapoda Macrura of Chile.—Lunds Universitets Arsskrift, new series 2, 47(10):1–109, figs. 1–19.

Huxley, T. 1879. On the classification and the distribution of the crayfishes.—Proceedings of the Zoological Society of London, 1878:752–788.

Jara, C. G. 1983. Segundo registro de *Parastacus araucanius* Faxon, 1914, (Crust: Decap: Macrura).—Archivos de Biología y Medicina Experimentales 16(2):R–163.

Manning, R. B., & H. H. Hobbs, Jr. 1977. Decapoda. Pages 157–162 *in* S. H. Hurlbert, ed., Biota acuática de Sudamérica austral. San Diego State University, San Diego, California, xiv + 342 pp.

Martens, E. von. 1869. Süd brasilische Süss und Brackwasser-Crustaceen nach den Sammlungen des Dr. Reinh. Hensel.—Archiv für Naturgeschichte 35(1):1–35.

McCoy, F. 1888. *Astacopsis serratus* (Shaw, sp.) var. *yarraensis* (McCoy).—Prodromus of the Zoology of Victoria 2:225–227, pl. 160.

Morgan, G. J. 1986. Freshwater crayfish of the genus *Euastacus* Clark (Decapoda, Parastacidae) from Victoria.—Memoirs of the Museum of Victoria 47(1):1–57, 23 figs.

Philippi, R. A. 1882. Zoología chilena.—Anales de la Universidad de Chile 61:624–628, 1 pl.

Poeppig, E. 1835. Reise in Chile, Peru und auf dem Amazonenstrome, während der Jahr 1827–1832. 1:xviii + 464 pp. [Reprinted 1960 in single volume with plates and atlas: xvii + 464 pp., Stuttgart: F. A. Brockhaus Komm.-Gesch.]

Reik, E. F. 1971. The freshwater crayfishes of South America.—Proceedings of the Biological Society of Washington 84(16):129–136.

Rudolph, E., & H. Rivas. 1988. Nuevo hallazgo de *Samastacus araucanius* (Faxon, 1914) (Decapoda: Parastacidae).—Biota (Osorno, Chile) 4:73–78.

van Straelen, V. 1942. A propos de la distribution des écrevisses, des homards et des crabes d'eau douce.—Bulletin du Musée Royal d'Histoire des Sciences Naturelles de Belgique 18(56):1–11.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 812–815

PANDALUS GURNEYI STIMPSON SYNONYMIZED WITH *PANDALUS DANAE* STIMPSON (DECAPODA: PANDALIDAE)

Mary K. Wicksten

Abstract.—*Pandalus gurneyi* Stimpson, 1871 is found to be a junior synonym of *P. danae* Stimpson, 1857. In all features that are supposed to distinguish between the two (number of rostral spines and teeth, length of rostrum/length of carapace, number of carpal articles of the second pereopods, length of scaphocerite/length of rostrum, and length/width of the sixth abdominal segment), there is considerable variability between individuals throughout the range. Specimens from southern California and Baja California tend to have fewer dorsal rostral spines, more ventral rostral teeth and fewer carpal articles than specimens from north of Point Conception, California. Small animals and functional males tend to have proportionally longer rostra than large females. *Pandalus gurneyi* may have been described from a male of *P. danae.*

The coonstripe shrimp, *Pandalus danae* Stimpson, 1857 is one of the most strikingly colored shrimp of low intertidal and shallow subtidal regions in Washington and British Columbia, on the northwestern coast of North America. The animal is marked with brown spots and stripes on a translucent background, with exceptionally vivid banding on the antennae and pereopods. Butler (1980) provided a more detailed description, color notes and illustration of the species. Ricketts et al. (1985) provided natural history notes on the shrimp, as did Kozloff (1973), who also included a black-and-white photograph. The popular books by Cribb (1983) and Rotman & Allen (1983) included color close-up photographs of the species.

Stimpson (1871) also described a second species, *Pandalus gurneyi.* The description consisted of a brief paragraph which stated that the species had a rostrum "more than one-half longer than the carapace" and armed above with 8–9 "teeth" and 9 ventral "teeth." Schmitt (1921) noted that the species was "very near *P. danae,*" and that it differed from *P. danae* in having a rostrum 1.5–1.66 times longer than the carapace, with 8–9 median dorsal movable spines and 9–10 immovable ventral spines. The right second pereopod had 17 carpal segments and the left, the longer of the two, 45 carpal segments. The sixth abdominal segment was 1.5 times as long as wide. (Schmitt used the terms "spines" and "segments" as quoted here, although later authors have called immovable spines "teeth" and carpal segments "carpal articles"). Stimpson's original description noted that the shrimp was "large" and that the "feet of the third pair . . . terminate in well-formed, subcheliform hands."

According to Schmitt, *P. gurneyi* ranged from Monterey to San Pedro and Santa Catalina Island, California, at 17–101 m, while *P. danae* ranged from Sitka, Alaska to San Francisco, California, at 18–186 m. However, Butler (1980) gave the range of *P. danae* south to Point Loma, California, from the intertidal zone to 185 m. There has been little mention of *P. gurneyi* in recent years except for inclusion in species lists or regional guides (Word & Charwat 1976,

Wicksten 1980), but *Pandalus danae* has been trawled off northern California (Wicksten 1984).

Recently, members of the Underwater Photographic Society (Los Angeles and Northern California Chapters) photographed pandalid shrimp in shallow intertidal areas from Monterey Bay south to the coast of Los Angeles and the nearby islands of southern Caifornia. I photographed and collected some of these pandalid shrimp in Monterey Bay, near Pacific Grove, and observed them off the Palos Verdes Peninsula, California. These animals differed in their color pattern slightly from that previously described for *P. danae* in that their stripes were not chocolate brown, but brick red. Their pereopods had bright yellow bands as well as brown and white ones, and the body bore bright blue spots as well as stripes of brown or white. However, Butler (1980) noted variation in the color pattern of *P. danae,* including these color marks.

Do these shrimp from California belong to one or two species of *Pandalus*? I undertook this study to determine which species were present, and whether or not there were consistent differences in color, morphology, range or habitat that could be used to distinguish between *P. danae* and *P. gurneyi.*

Methods

I examined 103 specimens previously identified as *P. danae* or *P. gurneyi,* from localities ranging from Puget Sound, Washington to Bahía San Quintín, Mexico. Specimens were from the collections of the Allan Hancock Foundation, University of Southern California (AHF); National Museum of Natural History (Smithsonian Institution), and Scripps Institution of Oceanography. Stimpson's type specimens no longer are in existence (presumably they were lost during the Chicago fire of 1871). However, I was able to examine specimens identified by W. L. Schmitt. The ratio of rostrum to carapace length, length versus width of the sixth abdominal segment, the number of rostral spines and their placement, the length of the antennal scale and the lengths and number of carpal articles of the second pereopod were reported and compared to determine whether there were any consistent differences between species.

Published photographs were examined to determine if there were any consistent differences in color between shrimp from Washington and British Columbia versus those from California. Color slides were taken by photographers Philip Turner of El off Pacific Grove and at the Monterey Bay Aquarium and Seattle Aquarium. Slides taken by photographers Philip Turner of El Cajón and Ken Howard of San Anselmo, California were examined.

Results

In all features that are supposed to differentiate *P. gurneyi* from *P. danae,* there is considerable overlap. Numbers of dorsal and ventral rostral teeth, rostrum/carapace length ratios, length/width ratios of the sixth abdominal segment, and numbers of carpal articles, are presented in Table 1. In the table, north-central California is defined as between the Oregon border and Point Conception; southern California is the coast south of Point Conception. There is considerable overlap in characters from area to area and between the figures reported for *P. danae* and *P. gurneyi.* As a general rule, the northernmost specimens had more dorsal rostral teeth, southern ones had more ventral teeth; and northern ones had more carpal articles than those to the south. Only a few animals had unusually high numbers of rostral spines or teeth: a single large female had 16 dorsal spines, and three specimens had 10 ventral teeth.

Small animals from southern California had the most variable form of rostrum. The shape ranged from nearly straight to strongly upcurved; the length, from less than the

Table 1.—Comparison of specimens of *Pandalus danae* by locality.

	Washington-Oregon	North-Central California	Southern California–Mexico
Number of dorsal rostral spines	9–13	7–16	7–11
Number of ventral rostral teeth	5–7	5–8	6–10
Average rostral formula	11/6	10/6	9/8
Rostrum/carapace	0.9–1.2	1.0–1.1	0.7–1.7
Length/width of sixth abdominal segment	1.6–2.0	1.2–1.6	1.1–2.0
Number of carpal articles of left second pereopod	57–67	55–60	47–59
Number of carpal articles of right second pereopods	22–27	18–21	15–23

carapace to twice its length. Small animals tended to have relatively larger rostral spines spaced more widely apart than larger animals. However, animals with long, upcurved rostra were found in the same samples as others with straight and shorter rostra, indicating that this variability was due to individual or age-related differences rather than to genetic or habitat-induced causes. Smaller animals also tended to have relatively longer antennal scales (scaphocerites), as long as the carapace, but the ratio of the length of the antennal scale to the carapace length varied from 0.7–1.0 throughout the range of *P. danae*.

As a general rule, coonstriped shrimp from Puget Sound and British Columbian waters had bands of dark chocolate brown on the body and appendages, and only white or translucent bands on the appendages. Shrimp from Monterey Bay and farther south tended to have brick red bands and bands of bright yellow on the appendages, as well as a few bright turquoise blue spots on the body. However, some larger individuals from Monterey Bay were translucent with very dark brown stripes, much like the animals from Puget Sound.

Discussion

The range of variability in all of the features that supposedly differentiate *P. gurneyi* from *P. danae* indicates that they are the same species, and that *P. danae* Stimpson, 1857 should take priority over *P. gurneyi* Stimpson, 1871. Holthuis (1980) noted that *P. franciscorum* Kingsley, 1878 also is a synonym of *P. danae*. In describing *P. gurneyi* as a distinct species, Stimpson probably was not aware that pandalid shrimp are protandrous hermaphrodites. Schmitt (1921) also may have been unaware that *Pandalus* species are sexually dimorphic, because hermaphrodism in *P. danae* was first described by Berkeley (1929). Butler (1980) noted that in male carideans, the rostrum generally is longer in proportion to the body than in females. In protandrous hermaphrodites, males also are smaller than females. It is noteworthy that two of Schmitt's specimens of *P. gurneyi* are functional males, with characteristic prehensile dactyls of the third pereopods (Butler 1980, fig. 4C) and flap-like endopods of the first pleopods. Stimpson's mention of "subcheliform hands of the third pair of legs" suggests that he also examined a male, although he did not indicate the sex of the specimen.

Differences in the numbers of rostral teeth and proportions of the body in *P. danae* may be due to changing water temperatures from the north to the south, or perhaps to genetic differences between populations within the species. Unlike the "geminate" species *Lebbeus catalepis* Jensen, of Puget Sound, and *L. lagunae* (Schmitt) of Monterey–Baja California, *P. danae* has a continuous geographic range along the entire

coast from Alaska to Baja California, including Oregon and northern California.

The cause of color differences observed in coonstriped shrimp is unknown, but may be related to diet, age, sex or habitat. Large animals usually are caught on coarse sand and gravel, but small ones can venture into eelgrass flats, docks, pilings, and cracks in rocky reefs. The shrimp can be found intertidally as far south as Bodega Bay, California (USC unpubl. field notes). Farther south, they live subtidally among cracks and rocks among kelp beds and breakwaters and on coarse sandy areas near reefs.

Examination of the specimens indicates that *Pandalus danae* extends south to the northwestern coast of Baja California, Mexico. The southernmost record to date is off Bahía San Quintín, Baja California Norte (30°20′N, 115°57′W), 41 m, 17 Oct 1971, R/V *Searcher* station 226, two specimens, AHF.

Literature Cited

Berkeley, A. A. 1929. Sex reversal in *Pandalus danae*.—American Naturalist 63:571–573.

Butler, T. H. 1980. Shrimps of the Pacific coast of Canada.—Canadian Bulletin of Fisheries and Aquatic Sciences 202:1–280.

Cribb, J. 1983. Treasures of the sea: marine life of the Pacific northwest.—Oxford University Press, Toronto, 96 pp.

Holthuis, L. B. 1980. FAO species catalogue. Vol. 1. Shrimps and prawns of the world.—FAO Fisheries Synopsis No. 125, 271 pp.

Kingsley, J. S. 1878. Notes on the North American Caridea in the Museum of the Peabody Academy of Science at Salem, Mass.—Proceedings of the Academy of Natural Sciences of Philadelphia 1878:89–98.

Kozloff, E. N. 1973. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago. University of Washington Press, Seattle, 282 pp.

Ricketts, E. F., J. Calvin, J. W. Hedgpeth, & D. W. Phillips. 1985. Between Pacific tides. Stanford University Press, 5th ed., 652 pp.

Rotman, J. L., & B. W. Allen. 1983. Beneath cold seas. Van Nostrand Reinhold, New York, 154 pp.

Schmitt, W. L. 1921. Marine decapod Crustacea of California.—University of California Publications in Zoology 23:1–470.

Stimpson, W. 1857. The Crustacea and Echinodermata of the Pacific shores of North America.—Journal of the Boston Society of Natural History 6:444–532.

———. 1871. Notes on North American Crustacea, in the museum of the Smithsonian Institution. No. III.—Annals of the Lyceum of Natural History of New York 10:92–136.

Wicksten, M. K. 1980. Crustacea and Pycnogonida. Pp. 196–223 *in* D. Straughan & R. W. Klink, compilers. A taxonomic listing of common marine invertebrate species from southern California.—Allan Hancock Foundation Technical Reports No. 3.

———. 1984. Distributions of some common decapod crustaceans and a pycnogonid from the continental shelf of northern California.—California Fish and Game 70:132–139.

Word, J. Q., & D. Charwat. 1976. Invertebrates of southern California coastal waters. II. Natantia. Southern California Coastal Water Research Project, El Segundo, 238 pp.

Department of Biology, Texas A&M University, College Station, Texas 77843, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 816–839

S. W. WILLISTON'S SPECIES OF EPHYDRIDAE (DIPTERA) FROM ST. VINCENT (WEST INDIES)

Wayne N. Mathis and James F. Edmiston

Abstract.—Lectotypes are designated for the following species: *Athyroglossa atra, Discomyza dubia, Athyroglossa nitida, Discocerina nana, Discocerina obscura, Discocerina facialis, Notiphila decorata, Notiphila bellula, Paralimna multipunctata, Paralimna obscura, Ilythea flavipes,* and *Scatella obscura.* Nomenclatural changes resulting from this study are as follows: *Dichaeta furcata* Coquillett is a junior synonym of *Notiphila decorata* Williston; *Psilopa nigropuncta* Williston is a junior synonym of *Psilopa girschneri* Von Röder; *Psilopa desmata* Williston is transferred to *Polytrichophora* where it is the senior synonym of *P. boriqueni* Cresson; *Hydrina nitifrons* Williston is transferred to *Hyadina*; and *Athyroglossa atra* Williston is accorded valid species status (previously it was listed as a junior synonym of *A. glaphyropus* Loew).

In 1896, Samuel Wendell Williston, then a professor of geology at the University of Kansas, published a rather remarkable monograph on the Diptera of St. Vincent. As a result, the dipterous fauna of St. Vincent remains one of the best studied in the Western Hemisphere. Williston's monograph included 161 genera and approximately 345 species, of which 256 were newly described. The vast majority of Williston's species are still valid, although many have been transferred to other genera, and in a few cases, other nomenclatural changes have resulted.

The thoroughness of Williston's treatment is likewise a testament to the excellent collecting of H. H. Smith, an American entomologist who was an experienced collector in the tropics and who was sent to the West Indies to assist the West Indian Committee (Papavero 1973). The Royal Society of England established this committee, and Smith was employed specifically to collect insects on these islands for the purpose of ". . . investigating the Flora and Fauna of the West Indies" (Williston 1896:253). Most of the collections that Smith made on St. Vincent were eventually deposited in the British Museum (Natural History) (now "The Natural History Museum"). The specimens of Diptera, however, were first sent to Professor Williston, who was a well-known dipterist in addition to being a professor of paleontology. Although Williston contributed much to our knowledge of St. Vincent's fauna, Diptera specifically, he never set foot on the island.

Among the 345 species of Diptera that comprise the monograph (the total also includes Aldrich's sections on the families Phoridae and Dolichopodidae), Williston included 26 species of Ephydridae, of which 24 were newly described. One species, *Drosophila pollinosa,* was described in the family Drosophilidae. Williston noted that this species was probably an ephydrid but preferred to describe it in *Drosophila* because some of its characters would (p. 414) " . . . lead one to search for the species in this genus." The species is now assigned to the ephydrid genus *Paratissa.* The two species that were described previously are *Cressonomyia aciculata* (Loew) and *Hydrochasma leucoproctum* (Loew).

The importance of Williston's monograph to the study of Ephydridae is several

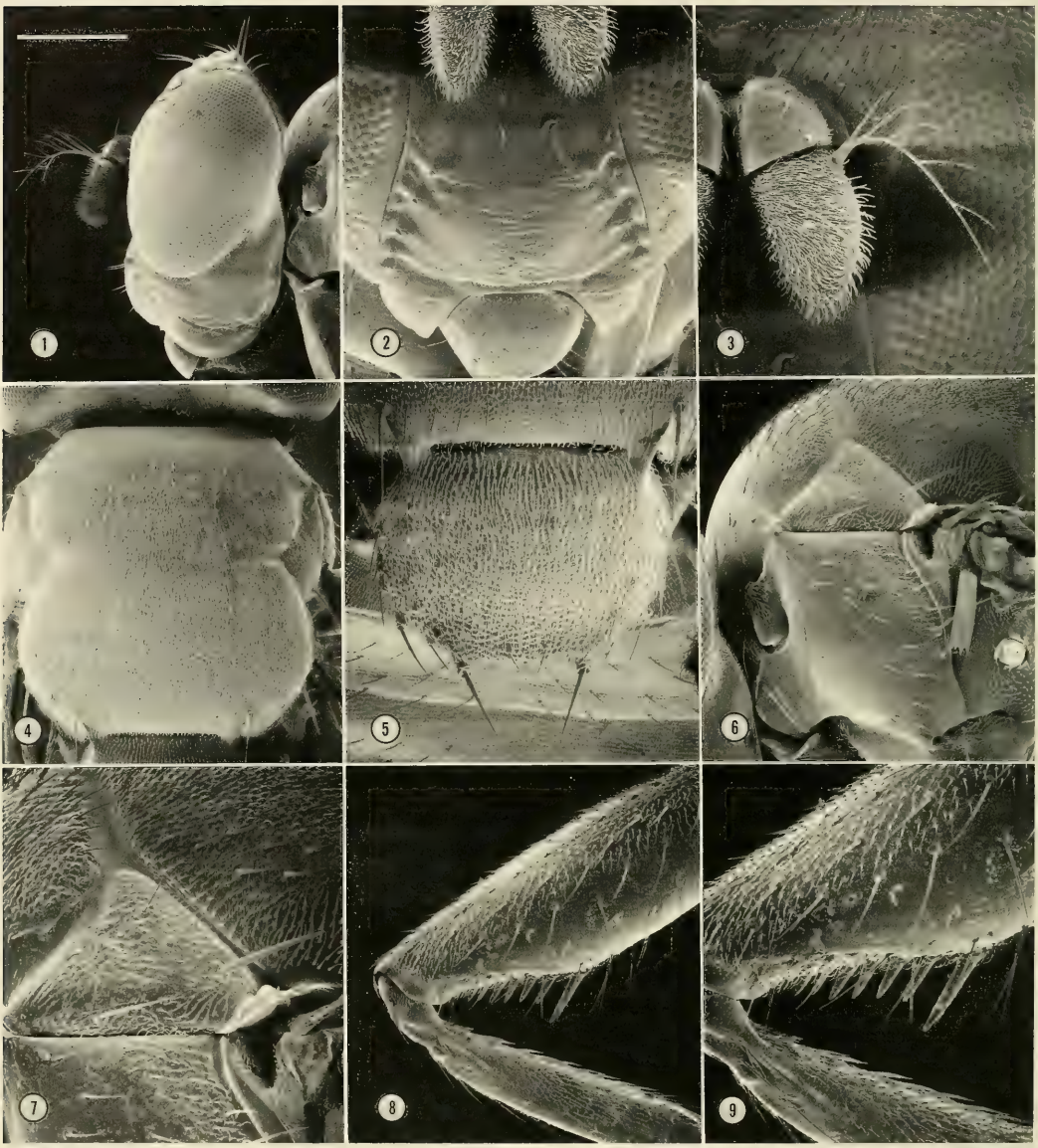
fold. Few 19th century treatments of Diptera included this many species of shore flies, which is all the more significant as St. Vincent is such a geographically restricted locality. The names Williston proposed, moreover, are relatively old in the nomenclatural history of the Ephydridae, especially for species occurring in the New World tropics. Being relatively old, the species names have been cited frequently in various studies. With few exceptions, however, the specimens from St. Vincent were not examined nor included in these studies. Thus the identities of species occurring elsewhere but determined as conspecific with those on St. Vincent must be considered questionable. This was not necessarily the fault of these workers, as possibilities for travel and study of the specimens Williston described were more limited then. Furthermore, travel to a single museum would not have been sufficient. Although the majority of specimens were deposited in London (BMNH), the rest of the collection was divided and is now deposited in the following American institutions: The University of Kansas, Lawrence (KU); American Museum of Natural History, New York (AMNH); and Cornell University, Ithaca, New York (CU). A further complication in assembling complete type series of Williston's species is the apparent loss of some specimens. This is especially critical for species that were originally represented by a single specimen, the holotype, or just a few specimens. As would be expected with limited access to collections and loss of specimens, errors in identification were made, and some of these have been perpetuated in the literature.

The first author is now working on two projects that concern the Caribbean fauna (the shore-fly faunas of the West Indies and Belizean Cays) and for which accurate determinations of Williston's species are essential. For better assurance of accurate identifications for these studies, we have attempted to examine all extant specimens included in the type series of Williston's species. We also conducted field work on St. Vincent to supplement the type series with freshly collected specimens, which, for *Paratissa pollinosa,* are the only extant specimens. The field work on St. Vincent resulted in numerous species that Williston did not report (nearly 25 thus far). The latter will be included in the more comprehensive faunal work noted previously. Our purpose here is to treat Williston's species, especially the nomenclatural changes that need to be properly documented for a forthcoming checklist of nearctic Ephydridae (Mathis 1992) and a world catalog (Mathis & Zatwarnicki, pers. comm.) that will be published before the faunal studies will be available.

St. Vincent is volcanic in origin and is part of the Windward chain of the West Indies (between the parallels of 13°23′–13°07′N and the meridians of 61°07′–61°17′W). The principal volcano, La Soufrière, is still active, last erupting in 1979, and was climbed as part of our field work there. St. Vincent and the Grenadines are a nation of islands with an area of nearly 390 sq km and a population of approximately 105,000. St. Vincent is situated in the Trade Wind Zone and has a Tropical Eastern Maritime climate (Harrison & Rankin 1976). Considerable topographical relief exists on the island (sea level to 923 m), resulting in localized variations in the climate between the windward and leeward coasts. St. Vincent and the Grenadines have been an independent nation since 1979. Formerly they were a British colony, which was their political affiliation during the 1890's when the faunal and floral surveys were conducted.

Methods and materials. —The species are treated in the sequence listed in recent catalogs (Wirth 1968a, Cogan 1980, Mathis 1989).

Label data, with the exception of primary types (lectotype designations in particular), are not cited for specimens bearing only general locality labels, such as "St. Vincent," which is the only label on many of



Figs. 1–9. Scanning electron micrographs of *Athyroglossa atra*: 1, Head, lateral view (0.27 mm); 2, Face, anterior view (136 μm); 3, Antenna, anterior view (100 μm); 4, Scutum, dorsal view (250 μm); 5, Scutellum, dorsal view (150 μm); 6, Notopleuron and katepisternum, lateral view (176 μm); 7, Notopleuron, lateral view (107 μm); 8, Fore femur and tibia, posterior view (120 μm); 9, Same (75 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 1.)

the specimens. Label data for primary types are quoted verbatim to better identify the exact specimen (particularly crucial for the lectotypes that are designated). A slash (/) in the citation of label data separates information on a label(s) if two or more labels are on a pin. Lectotype specimens were selected on the basis of the best specimen of the original type series that could readily be identified, regardless of gender. Frequently,

however, all syntypes were of one gender, leaving no alternative in that regard.

Other specimens that were collected in conjunction with recent field work on St. Vincent were examined as part of this study and are listed with the appropriate species to document the species' continuance and distribution on the island. The specimens are deposited in the following institutions (acronyms used in text are noted in parentheses): American Museum of Natural History, New York, USA (AMNH); The Natural History Museum, London, England (BMNH); Hungarian Natural History Museum, Budapest, Hungary (HNHM): National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM); Museum of Zoology and Entomology, Lund University, Lund, Sweden (ZIL).

The only two specific localities that Williston mentioned for species of Ephydridae are "Perseverance Valley" for *Ephydra pygmaea* and "near the sea by open stream" for *Psilopa desmata.* None of the specimens bearing determination labels of either species now has these locality data. The specimens apparently from Perseverance Valley, however, usually have a label indicating elevation, which varies from "500 feet." to "1000 ft." There are other specimens that are also labeled "500 feet" or "1000 feet," and we suspect that they too were collected in Perseverance Valley.

1. *Athyroglossa* (*Athyroglossa*) *atra* Williston, revised status
Figs. 1–12

Ochtheroidea atra Williston, 1896:401.

Athyroglossa atra.—Cresson, 1946:133 [generic combination].

Athyroglossa glaphyropus of authors, not Loew.—Wirth, 1968a:3 [misidentification, synonymy with *A. atra*].

Type material.—The lectotype female (designated here) is labeled "Co-type [circular label with a yellow border]/St. Vincent, W.I. H. H. Smith/W. Indies. 1907–66./Ochtheroidea atra Will [handwritten, two red submarginal borders]/LECTOTYPE Ochtheroidea atra Will. By W.N.Mathis [handwritten except for "LECTOTYPE" and "By", black sub-border]." The lectotype is double mounted (pin in a rectangular piece of cardboard), is in good condition, and is deposited in the BMNH. There are also eight paralectotypes as follows: BMNH (1 ♂, 4 ♀), KU (1 ♂), AMNH (1 ♂, 20324; 1 ♀, "Leeward near sea. By open Stream. Sept." [handwritten], 20322). Williston, in the original description, noted that there were "Twelve specimens."

Other specimens examined from St. Vincent.—Charlotte Parish: Montreal, 26 Mar 1989, A. Freidberg (1 ♀; USNM). St. Andrew Parish: Camden Park, 25 Mar 1989, A. Freidberg (2 ♀; USNM). St. David Parish: Richmond Beach, 28 Mar 1989, A. Freidberg (1 ♂; USNM). St. Patrick Parish: Cumberland Bay, 28 Mar 1989, A. Freidberg, W. N. Mathis (7 ♂, 8 ♀; USNM).

Distribution.—Neotropical: Colombia, Costa Rica, Ecuador, El Salvador, Mexico (Chiapas, Guerrero, Veracruz, San Luis Potosí), Panama, Venezuela, West Indies (Barbados, Dominica, Grenada, Jamaica, St. Vincent, Trinidad).

Remarks.—This is the type species of *Ochtheroidea* Williston. Wirth (1968a:3) synonymized this species with *Athyroglossa glaphyropus* Loew. We have examined the primary types of both names, however, and do not feel that they are conspecific (also see "Remarks" section of the next species, *A. dubia*).

This species is distinguished from congeners by the following combination of characters: arista with 4–5 dorsal branches (Figs. 1, 3); scutellum subquadrate, granulose, marginal setae 4–5 on each side, short and arising from distinct tubercles (Fig. 5); wing lightly infuscate generally, especially over crossvein dm-cu and at apex; halter whitish; mid and apical portion of hind tibiae yellowish; abdominal terga 1–4 flattened

Figs. 10–12. Scanning electron micrographs of *Athyroglossa atra*: 10, Abdomen, lateral view (200 μm); 11, Abdomen, dorsal view (0.43 mm); 12, Second tergum, dorsal view (150 μm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 10.)

dorsally and creased at dorsolateral margin (Fig. 10).

2. *Athyroglossa* (*Athyroglossa*) *dubia* (Williston), revised status
Figs. 13–21

Discomyza dubia Williston, 1896:392.—Wirth, 1968a:3 [neotropical catalog; synonymy with *A. glaphyropus* Loew].

Type material.—The lectotype male of *Discomyza dubia* (designated here) is labeled "Cotype [circular label with a yellow border]/Windward side St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./Discomyza dubia Will [handwritten, two red submarginal borders]/LECTOTYPE Discomyza dubia Will. ♂ By W.N.Mathis [handwritten except "LECTOTYPE" and "By", black submarginal border]." The lectotype is double mounted (pin in a rectangular piece of cardboard), is in good condition, and is deposited in the BMNH. There are also 27 paralectotypes as follows: BMNH (13 ♂, 10 ♀), KU (3 ♂, 1 ♀ "500 feet."). In the original description, Williston mentioned that there were "Numerous specimens."

Other specimens examined from St. Vincent.—Charlotte Parish: Colonarie River (2 km W South Rivers, 225 m), 13 Jul 1989, M. Sorensson, B. Mårtensson (1 ♂, 3 ♀; ZIL). St. Andrew Parish: Camden Park, 25 Mar 1989, A. Freidberg, W. N. Mathis (1 ♂, 1 ♀; USNM). St. Patrick Parish: Wallilabou (beach), 27 Mar 1989, W. N. Mathis (1 ♂; USNM).

Distribution.—Neotropical: West Indies (St. Vincent).

Remarks.—This species is distinguished from congeners by the following combination of characters: face at narrowest point between eyes narrow, width subequal to combined length of pedicel and 1st flagellomere; face with depressions laterally in which facial setae are inserted and with a moderately broad, vertical stripe that is distinctly granulose (Fig. 14); genal height at ventral margin of eye short, about equal to length of 1st flagellomere; first flagellomere concolorous with black pedicel; wing hyaline; halter whitish; mid and hind tibiae yellowish.

Like the preceding species, Wirth (1968a: 3) listed the name of *Discomyza dubia* as a junior synonym of *Athyroglossa glaphyropus* Loew. We have reexamined the primary types of both names (two syntype males from the MCZ for *A. glaphyropus*) and in each case have determined that they represent distinct species. The species are easily distinguished by the surface texture of the face. Specimens of *A. dubia* have a distinctly granulose, median, vertical stripe that is relatively broad (equal to width of pedicel), whereas in *A. glaphyropus,* the face has some surface texture that is rather vague, not dis-

Figs. 13–21. Scanning electron micrographs of *Athyroglossa dubia*: 13, Head, lateral view (200 μm); 14, Face, anterior view (100 μm); 15, Antenna, anterior view (86 μm); 16, Thorax, lateral view (200 μm); 17, Notopleuron, lateral view (86 μm); 18, Mesonotum, dorsal view (200 μm); 19, Scutellum, dorsal view (120 μm); 20, Abdomen, lateral view (200 μm); Abdomen, dorsal view (0.30 mm). (Scale lengths in parentheses; bar scale for all photographs = Fig. 13.)

tinctly granulose, and the overall facial appearance is mostly smooth and subshiny.

3. *Athyroglossa* (*Athyroglossa*) *nitida* Williston

Athyroglossa nitida Williston, 1896:397.

Athyroglossa (*Athyroglossa*) *nitida*.—Wirth, 1968a:3 [neotropical catalog].

Type material.—The lectotype female (designated here) is labeled "Windward side St. Vincent, W.I. H. H. Smith./Co-type [circular label with a yellow margin]/W.Indies.

1907–66./Athyroglossa nitida Will [handwritten, two red submarginal borders]/ LECTOTYPE Athyroglossa nitida Will. ♀ By W.N. Mathis [handwritten except for "LECTOTYPE" and "By", black sub-border]." The lectotype is double mounted (pin in a rectangular cardboard), is in good condition, and is in the BMNH. There is also a paralectotype female in the BMNH. Williston, in the original description, noted "Two specimens [♂, ♀]. St. Vincent."

A third specimen, a male from AMNH, is labeled "TYPE No. A. M. N. H. [red]/ Am. Mus. Nat. Hist. Dept. Invert. Zool. No. 20319a [number handwritten, "a" in pencil]." This specimen is double mounted (minute nadel in a heavy paper base, and is in good condition.

Williston noted two specimens (a male and female syntype) in the original description, but there are three specimens that are now labeled as syntypes: two females in the BMNH and a male in the AMNH. As the collections from St. Vincent were deposited primarily in the BMNH, we are assuming that the two specimens there are the original syntypes and that the male from the AMNH was identified later, then labeled as a "TYPE," and is not part of the type series. The male at the AMNH is conspecific with the two females.

Other specimens examined from St. Vincent.—St. Andrew Parish: Camden Park, 25 Mar 1989, A. Freidberg (2 ♂, 1 ♀; USNM).

Distribution.—Neotropical: Bolivia, Colombia, Costa Rica, Ecuador, El Salvador, Guyana, Mexico, Panama, Peru, Venezuela, West Indies (Cuba, Dominica, Puerto Rico).

Remarks.—This species is distinguished from congeners by the following combination of characters: face conically prominent below antennal grooves; face almost entirely smooth; arista with 5–6 dorsal branches; wing lightly infuscate; halter whitish to yellowish; tibiae mostly black, at most with apex of mid and hind legs yellowish.

4. *Ochthera cuprilineata* Wheeler

Ochthera cuprilineata Wheeler, 1896:123.—Clausen, 1977:486–492 [revision and lectotype designation].

Ochthera cuprilineata Williston, 1896:402 [preoccupied, Wheeler, 1896].—Wirth (1968a:21) listed this species as being valid.

Ochthera humilis Williston, 1897:6.—Cresson, 1938:36.—Clausen, 1977:486 [synonymy].

Ochthera melanderi Cresson, 1944:8.—Sturtevant & Wheeler, 1954:233 [review].—Clausen, 1977:486 [synonymy].

Type material.—Lectotype female of *O. cuprilineata* Wheeler (designated by Clausen 1977:488) is labeled "[brown square label without any writing]/St. Vincent W. Indies/W.M. Wheeler, Collection./Ochthera cuprilineata, Will. [handwritten]/LECTOTYPE Ochthera cuprilineata Wheeler ♀ Det. P.J. Clausen, 1973 [handwritten except "LECTOTYPE," red]." The lectotype is double mounted (pin in a rectangular cardboard), is in fair condition (wings missing), and is deposited in the AMNH. Two paralectotypes are deposited in the BMNH. In the original description, Williston noted "Eight specimens."

The lectotype males (both specimens designated by Clausen 1977:488) of *O. humilis* (Brazil. Rio de Janeiro: Rio de Janeiro) and *O. melanderi* (USA. California: Riverside Co., Riverside) are deposited in the ANSP.

Distribution.—Nearctic: USA (AZ, CA, NM, OK, TX). Neotropical: Argentina, Brazil, Canal Zone, Costa Rica, Mexico, Honduras, Guatemala, Panama, Ecuador, Paraguay, Peru, Trinidad, West Indies (Puerto Rico, St. Vincent).

Remarks.—This species is unique among congeners in having a single, black, facial spot that is vertically elongate, tapered both dorsally and ventrally, and sometimes with a purplish luster.

5. *Allotrichoma* (*Pseudohecamede*) *abdominale* (Williston)

Hecamede abdominalis Williston, 1896:398.
Allotrichoma abdominale.—Williston, 1897: 4 [generic combination].
Pseudohecamede abdominalis.—Hendel, 1936:106 [generic combination].—Wirth, 1956:4 [review, Bahamas]; 1965:737 [nearctic catalog]; 1968a:5 [neotropical catalog].
Allotrichoma (*Pseudohecamede*) *abdominale.*—Mathis, 1991:8–14 [revision].
Allotrichoma longirostre Hendel, 1930:135 [Bolivia].—Wirth, 1968a:5 [synonymy].

Type material.—Williston, in the original description of H. abdominalis, noted "Five specimens. St. Vincent." Two female syntypes of *Hecamede abdominalis* Williston were examined as part of this study. The first is labeled "Co-type [disk with yellow margin]/St. Vincent. W.I. H. H. Smith./W. Indies. 1907-66./+ [handwritten on a nearly square label/May/Hecamede abdominalis Will [handwritten, red sub-border]." The second female syntype is labeled "Co-type [disk with yellow margin]/Windward side St. Vincent. W.I. H. H. Smith./W. Indies. 1907–66./Hecamede abdominalis Will [handwritten, red sub-border]." Each of the two syntypes is double mounted (minute nadel in a small rectangular card on its edge), is in poor condition (the head is missing on both), and is deposited in BMNH. Because the syntypes are in poor condition, and critical characters for identification (structures of the male terminalia) are not found in females, we have not elected to designate a lectotype for this species. We have collected and studied several males from St. Vincent, the type locality, and these are conspecific.

The lectotype male of *A. longirostre* (Bolivia. Fortin Esteros; designated by Mathis 1991:9) is deposited in the Staatliches Museum für Naturkunde, Stuttgart, Germany.

Other specimens examined from St. Vincent.—St. Andrew Parish: Buccament Bay, 25–28 Mar 1989, W. N. Mathis (2 ♂, 6 ♀; USNM). St. David Parish: Richmond Beach, 28 Mar 1989, W. N. Mathis (2 ♂; USNM). St. George Parish: Kingstown, Botanical Garden, 25–27 Mar 1989, W. N. Mathis (6 ♂, 2 ♀; USNM); Yambou Head, 27 Mar 1989, W. N. Mathis (1 ♂, 2 ♀; USNM). St. Patrick Parish: Cumberland Bay, 28 Mar 1989, A. Freidberg (1 ♂, 1 ♀; USNM); Wallilabou (beach), 27 Mar 1989, W. N. Mathis (3 ♂, 1 ♀; USNM).

Distribution.—Nearctic: USA (AL AZ, AR, CA, FL, GA, MD, OH, TX, VA, WA). Neotropical: Argentina, Bahamas, Belize, Bolivia, Brazil, Costa Rica, Ecuador, El Salvador, Mexico, Panama, Paraguay, Peru, Venezuela, West Indies (Dominca, Guadeloupe, Jamaica, St. Vincent, Trinidad).

Remarks.—The distinctive, silvery-gray, horizontal stripe, which extends from the postpronotum through the ventral portion of the notopleuron, and the bicolored anepisternum usually distinguish this species from most congeners. To distinguish this species from *A. baja* Mathis or *A. ecuadorense* Mathis with which it is very similar, characters of the male terminalia need to be examined (see Mathis 1991, for figures).

6. *Ptilomyia parva* (Williston)

Hydrellia parva Williston, 1896:399.
Ptilomyia enigma Coquillet, 1900b:262.—Wirth, 1968a:4 [synonymy].
Ptilomyia parva.—Wirth, 1968a:4 [neotropical catalog: generic combination].

Type material.—The holotype male of *Hydrellia parva* is labeled "Type [circular label with a red border]/St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66.[a gray square label]/May/Hydrellia parva Will [handwritten, two red submarginal borders]." The holotype is double mounted (pin in a rectangular piece of cardboard), is in good condition, and is deposited in the BMNH.

The holotype female of *Ptilomyia enigma*

(West Indies. Puerto Rico) is deposited in the USNM (4379).

Other specimens examined from St. Vincent.—Charlotte Parish: Colonarie beach, 29 Mar 1989, W. N. Mathis (1 ♂; USNM). St. Andrew Parish: Buccament Bay, 25–28 Mar 1989, W. N. Mathis (10 ♂; 10 ♀; USNM); Camden Park, 25 Mar 1989, W. N. Mathis (6 ♂; 3 ♀; USNM). St. George Parish: Yambou Head, 27 Mar 1989, W. N. Mathis (7 ♂, 4 ♀; USNM). St. Patrick Parish: Cumberland Bay, 28 Mar 1989, W. N. Mathis (4 ♂; 3 ♀; USNM).

Distribution.—Nearctic: USA (AK, FL, GA, NM, MO, OH, SC, TX, VA). Neotropical: Bahamas, Bolivia, Costa Rica, Ecuador, El Salvador, Mexico, Panama, West Indies (Grenada, Dominica, Jamaica, Puerto Rico, St. Vincent, Trinidad).

Remarks.—This species is distinguished by the lack of a well-developed, presutural, dorsocentral seta; the mostly hyaline wing (lacking transverse bands but crossvein dm-cu infuscate) the sparsely microtomentose mesonotum and abdomen, which are dark brown and subshiny, and the larger dorsocentral and acrostichal setae at the sutural level.

7. *Discocerina* (*Basila*) *nana* Williston

Discocerina nana Williston, 1896:396.
Discocerina (*Basila*) *nana.*—Wirth, 1968a: 7 [neotropical catalog; listed as being valid in the subgenus *Basila*].

Type material.—The lectotype male (designated here) is labeled "Co-type [circular label with a yellow border]/1000 feet/[a black, square label]/St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./Discocerina nana Will. [handwritten, two red submarginal borders]/LECTOTYPE Discocerina nana Will. ♂ By W.N.Mathis [handwritten except for "LECTOTYPE" and "By", black sub-border]." The lectotype is double mounted (pin in a rectangular piece of cardboard), is in good condition, and is deposited in the BMNH. There are also eight paralectotypes as follows: BMNH (5 ♂, 1 ♀), AMNH (1 ♂, 1 ♀). Williston, in the original description, noted that the type series included "Numerous specimens."

Two paralectotypes (1 ♂, 1 ♀) are in the AMNH. The male paralectotype is labeled "[rectangular piece of paper, black on dorsal surface]/1000 feet [probably from Perseverence Valley]/TYPE No. A. M. N. H. [red]/Am. Mus. Nat. Hist. Dept. Invert. Zool. No. 20320 [number handwritten]/Discocerina nana Will [handwritten, apparently by Williston]." The female paralectotype bears the same type label, museum label (but with number 20321), and determination label.

Other specimens examined from St. Vincent.—St. Patrick Parish: Hermitage (6 km E Spring Village at Cumberland River, 550 M), 9 Jul 1989, M. Sorensson, B. Mårtensson (8 ♂, 2 ♀; ZIL).

Distribution.—Neotropical: Costa Rica, Colombia, West Indies (Dominican Republic, Dominica, Grenada, Puerto Rico, St. Vincent).

Remarks.—This species is distinguished from congeners, especially other species of the subgenus *Basila,* by the following combination of characters: facial series of setae 2 on each side; face distinctly two toned, a narrow, bare, shiny, vertical stripe that is bordered laterally by dense, lightly golden-white microtomentum; parafacials very narrow; frons also two toned, parafrons and narrowly triangular ocellar triangle densely microtomentose, blackish, appearing velvety, distinctly contrasted with remainder of frons which is lightly grayish blue; antenna mostly yellowish, pedicel and 1st flagellomere with some dark coloration anterodorsally; mesonotum almost uniformly colored and invested with light dusting of microtomentum, lacking distinct stripes or isolated spots; supra-alar seta lacking; and wing hyaline.

8. *Discocerina* (*Lamproclasiopa*) *obscura* Williston

Discocerina obscura Williston, 1896:397.
Discocerina (*Lamproclasiopa*) *obscura.*—Wirth, 1968a:8 [neotropical catalog].

Type material.—The lectotype male (designated here) is labeled "Co-type [circular label with a yellow border]/Windward side St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./1000 feet/[black square]/Discocerina obscura Will [handwritten, two red submarginal borders]/LECTOTYPE Discocerin obscura Will. ♂ By W.N.Mathis [handwritten except for "LECTOTYPE" and "By", black sub-border]." The lectotype is deposited in the BMNH. There are also 19 paralectotypes as follows: BMNH (10 ♂, 5 ♀), KU (2 ♀ "Kingstown" and "500 feet."), AMNH (2 ♂, 20323, "500 feet" and "1000 feet"). Williston, in the original description, noted that there were "Numerous specimens." In the AMNH there is also one specimen that is apparently a paralectotype from "Kingstown" (sex undetermined, abdomen removed, 20317).

Other specimens examined from St. Vincent.—Charlotte Parish: Colonarie River (2 km W South Rivers, 225 m), 13 Jul 1989, M. Sorensson, B. Mårtsensson (7 ♂, 1 ♀; ZIL); Montreal, 26 Mar 1989, W. N. Mathis (1 ♂, 4 ♀; USNM). St. Andrew Parish: Camden Park, 25 Mar 1989, W. N. Mathis (4 ♂, 1 ♀; USNM). St. George Parish: Kingstown, Botanical Garden, 25–27 Mar 1989, W. N. Mathis (25 ♂, 2 ♀; USNM). St. Patrick Parish: Cumberland Bay, 28 Mar 1989, A. Freidberg, W. N. Mathis (2 ♀; USNM); Wallilabou (beach), 27 Mar 1989, W. N. Mathis (1 ♂; USNM).

Distribution.—Nearctic: USA (FL, GA, LA, NY). Neotropical: Brazil, Panama, West Indies (Cuba, Dominca, Puerto Rico, St. Vincent).

Remarks.—This species is distinguished from congeners, especially those of the subgenus *Lamproclasiopa,* by the following combination of characters: facial series of setae 3 on each side; face unicolorous, invested with whitish microtomentum; parafacials lacking setulae; frons uniformly lightly microtomentose, lacking distinctive bluish or greenish stripes; mesonotum uniformly subshiny, with light investment of brown microtomentum, lacking shiny surfaces with metallic luster; supra-alar seta present; anterior notopleural seta inserted much closer to posterior seta and to postpronotal seta; and abdomen similar in color and with only slightly more microtomentum than mesonotum.

9. *Hydrochasma faciale* (Williston)

Discocerina facialis Williston, 1896:396.
Hydrochasma faciale.—Wirth, 1968a:8 [neotropical catalog; generic combination].
Hydrochasma zernyi Hendel, 1936:103.—Wirth, 1968a:8 [synonymy].
Hydrochasma capax Cresson, 1938:26.—Wirth, 1968a:8 [synonymy].

Type material.—The lectotype male (designated here) is labeled "Co-type [circular label with a yellow border]/Windward side St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./Discocerina facialis Will. [handwritten, two red submarginal borders]/LECTOTYPE Discocerina facialis Will. ♂ By W.N.Mathis [handwritten except for "LECTOTYPE" and "By", black sub-border]." The lectotype is double mounted (pin in rectangular piece of cardboard), is in poor condition (right foreleg, mid legs missing), and is deposited in the BMNH. There is also one female paralectotype (BMNH). Williston, in the original description, noted "Five specimens. St. Vincent." The other syntypes (1 ♂, 2 ♀, BMNH) are apparently representatives of a H. incisum (no silvery triangular patches on dorsum of abdomen).

The syntypes of *Hydrochasma zernyi* (Brazil. Pará: Santarém) are deposited in the NMW.

The holotype female of *Hydrochasma capax* (Guatemala. Gualan) is deposited in the ANSP (6533).

Other specimens examined from St. Vincent.—Charlotte Parish: Colonarie (beach), 29 Mar 1989, W. N. Mathis (2 ♂; USNM). St. Andrew Parish: Buccament Bay, 25–28 Mar 1989, W. N. Mathis (6 ♂, 15 ♀; USNM). St. David Parish: Richmond Beach, 28 Mar 1989, W. N. Mathis (1 ♀; USNM). St. Patrick Parish: Cumberland Bay, 28 Mar 1989, A. Freidberg, W. N. Mathis (5 ♂, 3 ♀; USNM); Wallilabou (beach), 27 Mar 1989, W. N. Mathis (5 ♂, 10 ♀; USNM).

Distribution.—Nearctic: USA (AZ, CA, TX). Neotropical: Argentina, Brazil, Ecuador, Guatemala, West Indies (Dominica, St. Vincent).

Remarks.—This species is distinguished from congeners by the following characters: antennal coloration almost evenly divided between yellowish and dark gray, dorsal and anterior surfaces of pedicel and 1st flagellomere extensively dark gray; parafacial silvery white, concolorous with facial coloration; fore femur bearing a distinctive, comb-like row of stout setulae along anteroventral surface; tibiae mostly gray; and abdomen lacking wedge-shaped silvery-gray areas.

We follow Wirth (1968a) in recognizing the two junior synonyms of *H. faciale,* as noted in the synonymy, but did not confirm the conspecificity of the appropriate primary types.

10. *Polytrichophora desmata* (Williston), new combination
Figs. 22–25

Psilopa desmata Williston, 1896:395.—Wirth, 1968a:9 [neotropical catalog; listed as an unrecognized species].

Polytrichophora boriqueni Cresson, 1930:77; 1946:143 [review].—Wirth, 1968a:8 [neotropical catalog]. new synonym.

Type material.—The holotype male of *Psilopa desmata* is labeled "Type [circular label with a red border]/Windward side St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./Psilopa desmata Will [handwritten, two red submarginal borders]." The holotype is double mounted (pin in a rectangular piece of cardboard), is in poor condition (head and right wing missing, mesonotum cracked anteriorly; abdomen removed, dissected, parts in an attached microvial), and is deposited in the BMNH.

The holotype male of *Polytrichophora boriqueni* (West Indies. Puerto Rico: Adjuntas) is deposited in the ANSP.

Other specimens examined from St. Vincent.—Charlotte Parish: Montreal, 26 Mar 1989, W. N. Mathis (1 ♂; USNM).

Distribution.—Neotropical: West Indies (Dominica, Puerto Rico, St. Vincent).

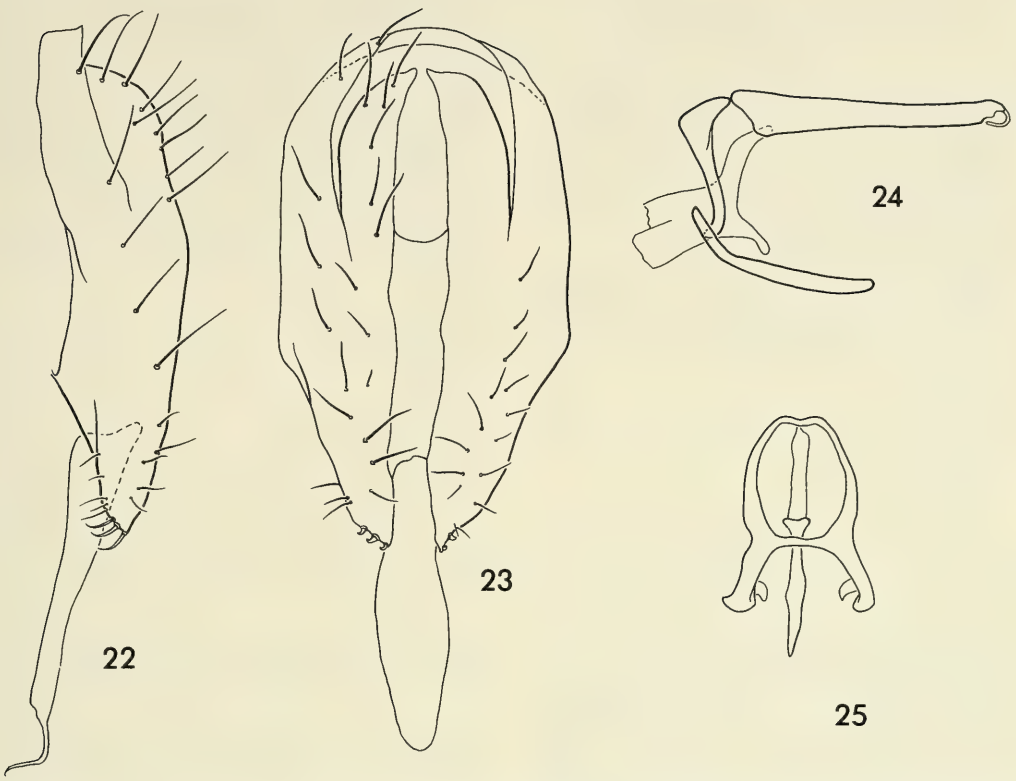
Remarks.—Williston, who commented on the specific locality of only one other species (*Ephydra pygmea*), noted that the holotype of the senior synonym was collected "Near the sea by open stream."

This species is distinguished from congeners by the following combination of characters: lower portion of fronto-orbits not differing significantly in color from parafacials; midfacies below midheight with broad, median area moderately microtomentose, appearing dull, grayish, contrasted with blackish, shinier, lateral margins of midfacies; parafacial color contrasted with the much darker midfacies; parafacies with little or no dilation ventrally; fore femur with distinct row of moderately short, stout setae along posteroventral surface; abdominal terga 1–4 subshiny, moderately microtomentose, blackish brown; 5th tergum of male distinctly more sparsely microtomentose and shinier than terga 1–4, black.

11. *Leptopsilopa nigrimana* (Williston)

Psilopa nigrimana Williston, 1896:393.

Leptopsilopa nigrimana.—Cresson, 1938:30 [generic combination].—Wirth, 1956:14 [review, Bahamas]; 1968a:10 [neotropical catalog].



Figs. 22–25. *Polytrichophora desmata*: 22, Epandrium, cerci, and aedeagus, lateral view; 23, Same, posterior view; 24, Internal genitalia, lateral view; 25, Hypandrium, ventral view.

Psilopa willistoni Cresson 1918:53 [unjustified new name for *Psilopa nigrimana* Williston, see Cresson 1938:31].

Leptopsilopa willistoni.—Curran 1928:61 [generic combination].

Type material.—The holotype female (not a male as Williston indicated) is labeled "Type [circular label with a red border]/ Windward side St Vincent, W.I. H. H. Smith./W.Indies. 1907–66./May/[gray square]/Psilopa nigrimana [handwritten, two red submarginal borders]." The holotype is double mounted (pin in a rectangular piece of cardboard), is in very poor condition (head, left wing, left hind leg missing, mesonotum cracked), and is deposited in the BMNH.

Other specimens examined from St. Vincent.—St. Andrew Parish: Buccament Bay, 25–28 Mar 1989, W. N. Mathis (1 ♀; USNM). St. David Parish: Richmond Beach, 28 Mar 1989, W. N. Mathis (2 ♂, 3 ♀; USNM). St. Patrick Parish: Cumberland Bay, 28 Mar 1989, A. Freidberg, W. N. Mathis (21 ♂, 13 ♀; USNM).

Distribution.—Widespread throughout the Bahamas, Mexico, the West Indies (Dominca, St. Vincent), and Central and South America.

Remarks.—This species is easily distinguished from congeners by the completely hyaline wing; the whitish yellow to ochraceous fore coxa and trochanter (remainder of foreleg black); and trochanter and distal half of middle and hind coxae, basal margin of middle and hind femora, middle and hind tibiae and tarsi, except 5th tarsomere, ochraceous.

12. *Paratissa pollinosa* (Williston)
Fig. 26

Drosophila pollinosa Williston, 1896:414.
Paratissa pollinosa.—Coquillett, 1900a:36 [generic combination].—Sturtevant, 1923: 10 [types apparently lost, not in London, New York, or Kansas].
Paratissa semilutea of authors (misidentification in part).—Wirth, 1965:740 [nearctic catalog; synonymy of *pollinosa* with *semilutea*]; 1968a:9 [neotropical catalog].
Hostis guamensis of authors (misidentification).—Adachi, 1952:353 [list from Hawaii].

Type material.—Williston, in the original description, noted "Two specimens. St. Vincent." Sturtevant (1923) was unable to locate either after searching through collections in the BMNH, KU, and AMNH. We were likewise unsuccessful in finding any syntypes and have had to base our characterization of this species on the neotype (designated here) that was recently collected on St. Vincent. The neotype is labeled "W.I. St. Vincent. Cumberland Bay[,] (13°16'N, 61°16'W)[,] 8–10 June 1991[,] W. N. & D. Mathis/NEOTYPE ♂ Drosophila pollinosa Williston designated by W.N.Mathis & J. Edmiston [handwritten, red]." Twenty-one neoparatypes (3 ♂, 18 ♀), which bear identical locality label data, are also designated. The neotype is double mounted (minuten in a block of plastic), is in excellent condition (some laboubenialies on mesonotum), and is deposited in the USNM.

Distribution.—Neotropics: Panama and the West Indies (Dominica, St. Lucia, St. Vincent); Oceania: Hawaii (Oahu and Maui) and Pitcairn.

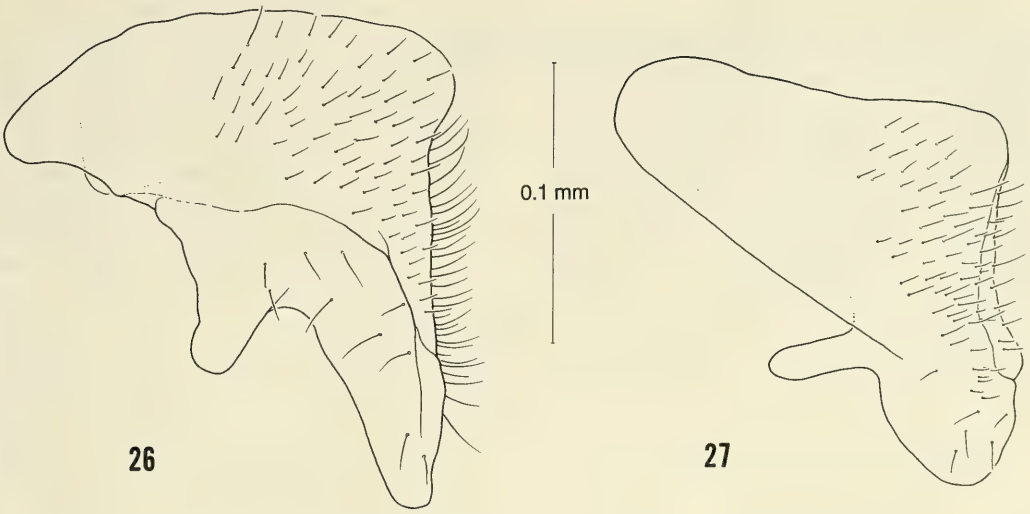
Remarks.—Williston (1896:414) stated that "In all probability the present species belongs among the Ephydridae, but the very flat face and the presence of vibrissae will lead one to search for the species in this genus." Williston's prediction came true, beginning with Coquillett (1900a), who assigned this species to *Paratissa.* Coquillett's precedent has been followed by all subsequent authors (see species synonymy), but without confirmation from study of the primary types, which were lost. We accept this precedent, which helped determine the designation of the neotype, but not the synonymy of *P. pollinosa* and *P. semilutea,* as there is more than one species in the Caribbean.

Externally this species is virtually identical to *P. semilutea,* and the two species have been confused with each other. The only differences that we are aware of that distinguish the two species are structures of the male terminalia (Figs. 26, 27), the shape of the surstylus and aedeagus in particular. These are as follows (Fig. 26): surstylus from a posterior view with the ventromedial angle acutely pointed, narrowly rounded in posteroventral view; the ventral spur has an oblique, ventromedial orientation, forming a distinct, V-shaped pocket (angle acute) between the spur and posteroventral projection; spur gradually tapered to bluntly rounded apex; and base of aedeagus, at juncture with narrow, parallel-sided apex, with sides angulate, forming a distinct shoulder on each side.

13. *Psilopa girschneri* von Röder

Psilopa girschneri von Röder, 1889:55.
Psilopa nigropuncta Williston, 1896:393.—Wirth, 1968a:9 [neotropical catalog; listed as being valid in the genus *Psilopa*]. new synonym.

Type material.—The holotype female of *P. nigropuncta* (not a male as Williston indicated) is labeled "Type [circular label with a red border]/Windward side St. Vincent, W.I. H. H. Smith/W.Indies. 1907–66./[maroon, square label]/May/Psilopa nigropuncta Will [handwritten, two red submarginal borders]." The holotype is double mounted (pin in a rectangular piece of cardboard), is in good condition, and is deposited in the BMNH.



Figs. 26, 27. Surstylus, posteroventral view: 26, *Paratissa pollinosa*; 27, *P. semilutea*.

The syntypes of *P. girschneri* (Germany. Artern, Sachsen) are deposited in the BMNH.

Distribution. —Australasian/Oceanian: Hawaiian Islands. Nearctic: Canada (QB), USA (AK, CA, CO, ID, TX, WA). Neotropical: Chile, Galápagos Archipelago, El Salvador. Oriental: Taiwan. Palearctic: Germany, Poland, Sweden.

Remarks. —This species is recognized by the investiture of silvery gray microtomentum on the face; the dark, mostly blackish femora and tibiae; and the dark spot at the apex of vein R4+5 (some specimens also have a darkened spot at the apex of vein M).

14. *Typopsilopa nigra* (Williston)

Psilopa nigra Williston, 1896:393.

Helaeomyia nigra. —Cresson, 1942:124 [generic combination].

Typopsilopa nigra. —Wirth, 1968a:13 [neotropical catalog; generic combination]; 1968b:234 [revision and lectotype designation].

Typopsilopa flavitarsis Cresson, 1916:147.—Wirth, 1968a:13 [neotropical catalog; synonymy].

Type material. —Lectotype female of *Psilopa nigra* (designated by Wirth 1968b:235) is labeled "Co-type [circular label with a yellow border]/St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./Psilopa nigra Will [handwritten, two red submarginal borders]/LECTOTYPE Psilopa nigra Will. ♀ By W.W.Wirth [handwritten except for "LECTOTYPE" and "By", black submarginal border]." The lectotype is double mounted (pin in a rectangular piece of cardboard), is in good condition, and is deposited in the BMNH.

The holotype male of *T. flavitarsis* (USA. Arizona: Mohave Co., Bill Williams Fork) is deposited in the Snow Collection (KU).

Distribution. —Nearctic: USA (AZ, CA, FL, GA, LA, VA). Neotropical: Bahamas, Brazil, British Guiana, Costa Rica, Mexico (La Bosa), Nicaragua, Panama, West Indies (Dominica, Puerto Rico).

Remarks. —Although Wirth's revision (1968b) was intended to be the first citation of the generic combination and synonymy noted, his catalog of the neotropical species of Ephydridae (1968a) was published first and is thus the proper reference for these actions.

This species is distinguished from congeners by the following combination of characters (males needed for most characters): tarsi of all legs at least partially pale; tarsomeres 1–4 of foreleg bright yellow; sternum 6 of male broader than distance across lobes of surstylus, heavily sclerotized and forming a broad concavity; surstylus deeply emarginate anteroventrally, with lateral lobes widely separated, low and angular, not as long as the distance between their distal points; male cerci with anteroventral end not spinelike.

15. *Notiphila decorata* Williston
Figs. 28–31

Notiphila decorata Williston, 1896:389.—Wirth, 1968a:14 [neotropical catalog; listed as an unrecognized species].

Dichaeta furcata Coquillett, 1902:182. new synonym.

Notiphila (*Agrolimna*) *furcata*.—Cresson, 1917:59 [generic combination].—Wirth, 1965:747 [nearctic catalog]; 1968a:14 [neotropical catalog].—Mathis, 1979:63–65 [revision].

Type material.—The lectotype female (designated here) is labeled "Co-type [circular label with a yellow border]/Leeward side St. Vincent, W.I. H. H. Smith./ W.Indies. 1907–66./N. decorata Will [handwritten in faint red ink]/LECTOTYPE Notiphila decorata Will. ♀ By W.N.Mathis [handwritten except for "LECTOTYPE" and "By", black submarginal border]." The lectotype is deposited in the BMNH. There is also one female paralectotype (BMNH). Williston, in the original description, noted "Two specimens."

The lectotype male of *D. furcata* (USA. Florida. Dade Co., Biscayne Bay; designated by Cresson 1917:59) is deposited in the USNM.

Other specimens examined from St. Vincent.—St. George Parish: Yambou Head, 27 Mar 1989, W. N. Mathis (1 ♂; USNM). St. Patrick Parish: Cumberland, 28 Mar 1989, A. Freidberg, W. N. Mathis (6 ♂, 6 ♀; USNM).

Distribution.—Nearctic: USA (AL, DE, FL, GA, LA, SC, TX, VA). Neotropical: West Indies (Dominica, St. Vincent).

Remarks.—This species is recognized by having four dorsally erect setae along the mid tibia; palpus orange to yellowish; antenna mostly blackish (first flagellomere sometimes reddish orange at base); arista with 10 or more dorsal branches; setal fascicle of hind basitarsus entirely pale; fourth tergum of male bearing a row of posterior marginal setae that are approximately twice the length of the tergum (Fig. 28); and fifth tergum of male produced posteriorly into a slender process that is equal in length to apical setae, this process bearing two long, apical setae (Fig. 28).

Identification and use of *N. decorata* supplants the better-known name of *N. furcata* Coquillett, which is also more descriptive of the unusual configuration and large setae of the male abdomen (see preceding paragraph). The species is clearly identifiable and easily recognized, and neither name is frequently used in the literature; thus the rule of priority is the advisable course.

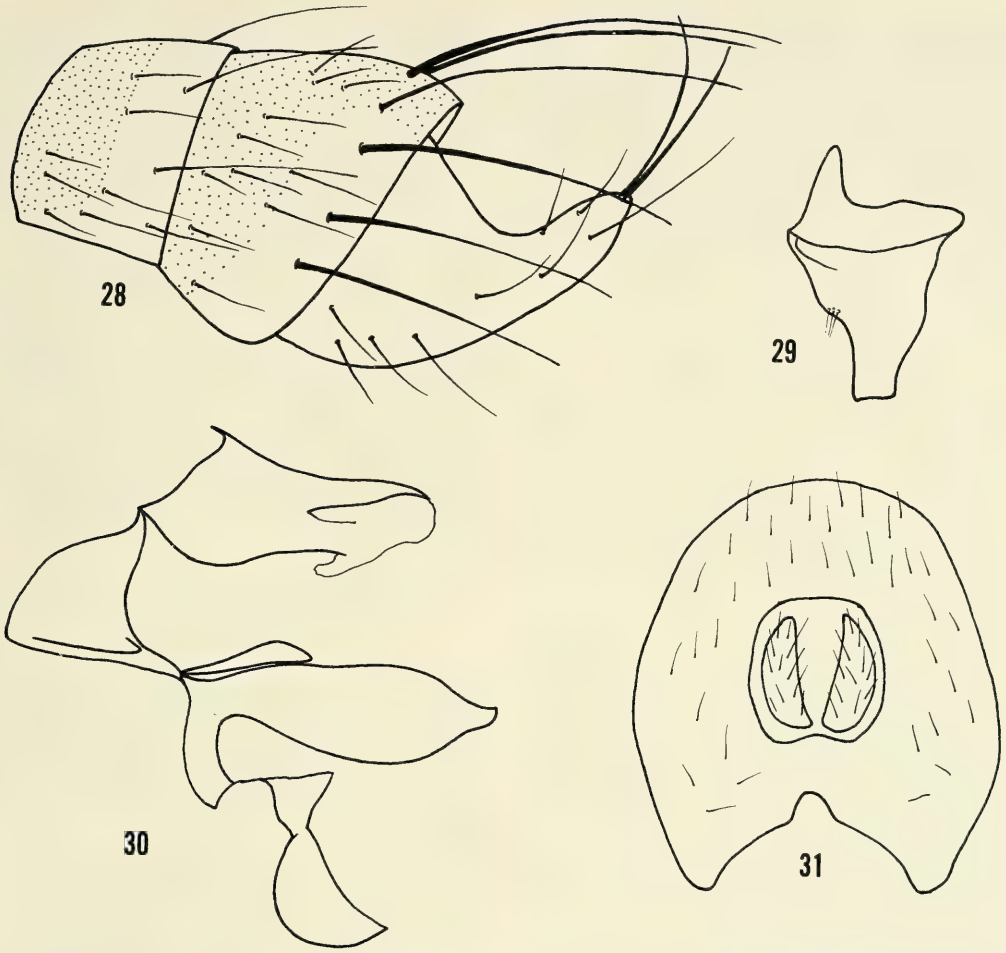
16. *Notiphila* (*Notiphila*) *erythrocera* Loew

Notiphila erythrocera Loew, 1878:194.

Notiphila bellula Williston, 1896:390.—Cresson, 1947:58 [synonymy].

Notiphila (*Notiphila*) *erythrocera*.—Wirth, 1968a:13 [neotropical catalog].

Type material.—The lectotype female of *N. bellula* (designated here) is labeled "Cotype [circular label with a yellow border]/ Leeward side St. Vincent, W.I. H. H. Smith./ W.Indies. 1907–66./Notiphila bellula Will. [handwritten, two red submarginal borders]/LECTOTYPE Notiphila bellula Will. ♀ By W.N.Mathis [handwritten except for "LECTOTYPE" and "By", black submarginal border]." The lectotype is double mounted (pin in a rectangular piece of card-



Figs. 28–31. *Notiphila decorata*: 28, Apex of abdomen, lateral view; 29, Surstylus, lateral view; 30, Internal male genitalia, lateral view; 31, Epandrium and cerci, posterior view.

board), is in good condition, and is deposited in the BMNH. There are also six female paralectotypes as follows: BMNH (3 ♀), CU (2 ♀, 2768.1 and 2768.2), AMNH (1 ♀, 20329). Williston, in the original description, noted "Ten specimens. St. Vincent."

The lectotype female of *N. erythrocera* (Cuba; designated by Mathis 1979:31) is deposited in the MCZ.

Other specimens examined from St. Vincent.—Charlotte Parish: Montreal, 26 Mar 1989, W. N. Mathis (6 ♂, 6 ♀; USNM). St. Andrew Parish: Buccament Bay, 25–28 Mar 1989, W. N. Mathis (3 ♂, 1 ♀; USNM). St. David Parish: Richmond Beach, 28 Mar 1989, W. N. Mathis (1 ♂, 2 ♀; USNM). St. George Parish: Yambou Head, 27 Mar 1989, W. N. Mathis (21 ♂, 8 ♀; USNM). St. Patrick Parish: Cumberland Bay, 28 Mar 1989, A. Freidberg, W. N. Mathis (4 ♀; USNM).

Distribution.—Nearctic: USA (AL, AZ, CA, CO, DA, FL, GA, LA, MD, NE, NV, NJ, NM, OR, SC, TX, UT, WY). Neotropical: widespread in central and South America, West Indies (Cuba, Dominica, Puerto Rico, St. Vincent).

Remarks.—This species is quite variable but can be distinguished from congeners by

the following combination of characters: antenna pale, yellowish orange, scape and pedicel often with some darkened areas; aristal rays 11–12; facial setae well developed but few in number 3–4 on each side; generally with a distinctive, brown pattern on the abdominal terga; and structures of male terminalia (see Mathis 1979, for figures).

17. *Paralimna* (*Paralimna*) *multipunctata* Williston

Paralimna multipunctata Williston, 1896: 390.—Wirth, 1956:17 [review, Bahamas].

Paralimna (*Paralimna*) *multipunctata.*—Wirth, 1968a:15 [neotropical catalog; listed as being valid in the subgenus *Paralimna*].

Type material.—The lectotype male (designated here) is labeled "Co-type [circular label with a yellow border]/Leeward side St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./Paralimna multipunctata Will [handwitten, faint red ink]/LECTOTYPE Paralimna multipunctata Will. ♂ By W.N. Mathis [handwritten except for "LECTOTYPE" and "By", black submarginal border]." The lectotype is double mounted (pin in a rectangular piece of cardboard), is in good condition, and is deposited in the BMNH. There are also 10 paralectotypes as follows: BMNH (2 ♂, 2 ♀, 1?), KU (1 ♂, 1 ♀), AMNH, (3 ♀, 20329a, 20327, 20327a). Williston, in the original description, indicated that there were "Numerous specimens."

Other specimens examined from St. Vincent.—St. Andrew Parish: Buccament Bay, 25–28 Mar 1989, W. N. Mathis (20 ♂, 5 ♀; USNM); Camden Park, 25 Mar 1989, A. Freidberg (1 ♂; USNM). St. George Parish: Yambou Head, 27 Mar 1989, W. N. Mathis (1 ♂, 2 ♀; USNM). St. Patrick Parish: Cumberland Bay, 28 Mar 1989, W. N. Mathis (1 ♂; USNM); Wallilabou (beach), 27 Mar 1989, W. N. Mathis (4 ♂, 1 ♀; USNM).

Distribution.—Nearctic: USA (CA, FL, TX). Neotropical: Costa Rica, Mexico, Nicaragua, Panama, Venezuela, West Indies (Bahamas, Cuba, Dominica, Grenada, Puerto Rico, St. Thomas, St. Vincent).

Remarks.—This species is distinguished from congeners by the following combination of characters: body generally bicolored, dorsum mostly brown to dark brown, lateral surfaces mostly gray, sometimes silvery white; eye round, about as wide as high; gena high, height subequal to length of first flagellomere; anepisternum and katepisternum concolorous, light yellowish gray; fore femur with anteroventral, comb-like row of flattened setae; and posteroventral surface of fore femur at basal one-half bearing irregular but distinct linear patch of setae.

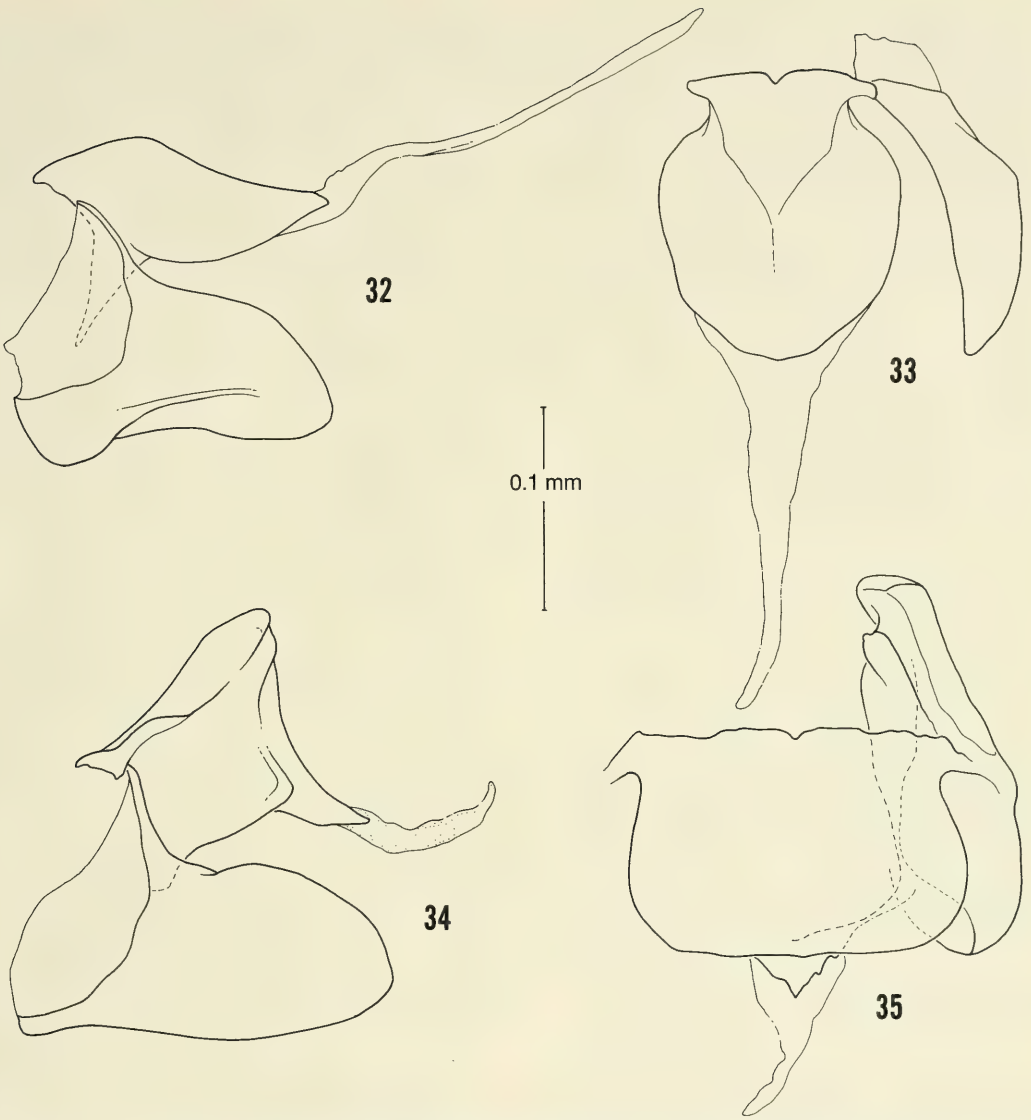
18. *Paralimna* (*Phaiosterna*) *obscura* Williston
Figs. 32, 33

Paralimna obscura Williston, 1896:39].

Paralimna (*Phaiosterna*) *obscura.*—Wirth, 1968a:16 [neotropical catalog; listed as being valid under the subgenus *Phaiosterna*].

Type material.—The lectotype male (designated here) is labeled "Co-type [circular label with a yellow border]/Leeward side St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./Paralimna brunnea [lined out] obscura Will. [handwritten, two red submarginal borders]/LECTOTYPE Paralimna obscura Will. ♂ By W.N.Mathis [handwritten except for "LECTOTYPE" and "By", black submarginal border]." The lectotype is double mounted (pin in a rectangular piece of cardboard), is in good condition, and is deposited in the BMNH. There are also 15 paralectotypes as follows: BMNH (4 ♂, 3 ♀), KU (3 ♂, "35" and "21"), AMNH (1 ♂, 4 ♀, 20326). Williston, in the original description, indicated that there were "Numerous specimens."

Other specimens examined from St. Vincent.—St. Vincent (2 ♂; CU; "Lot. 662 Sub. 75"; one of the males lacks its head. The



Figs. 32–35. *Paralimna obscura*: 32, Gonite (right) and aedeagus, lateral view; 33, Aedeagus and gonite (left), dorsal view. *P. decipiens*: 34, Gonite (right) and aedeagus, lateral view; 35, Aedeagus and gonite (left), dorsal view.

determination label, which is handwritten, reads "Paralimna brunnea Will. [cursive] mss. may be obscura"). Charlotte Parish: Montreal, 26 Mar 1989, A. Freidberg (1 ♂, 1 ♀; USNM). St. Andrew Parish: Buccament Bay, 25–28 Mar 1989, W. N. Mathis (5 ♂, 6 ♀; USNM); Camden Park, 25 Mar 1989, W. N. Mathis (7 ♂, 2 ♀; USNM). St. David Parish: Richmond Beach, 28 Mar 1989, W. N. Mathis (2 ♂; USNM). St. George Parish: Yambou Head, 27 Mar 1989, W. N. Mathis (5 ♂, 2 ♀; USNM).

Distribution.—Nearctic: Bermuda, USA (CA, FL, TX). Neotropical: Argentina, Bolivia, Brazil, Costa Rica, Ecuador, Mexico, Panama, Paraguay, West Indies (Cuba, Gre-

nada, Jamaica, Puerto Rico, St. Vincent, Virgin Islands).

Remarks.—This species and *P. decipiens* Loew are closely related and are very similar in appearance. Externally we have difficulty in distinguishing between them due to variation in coloration and microtomentum. Both species can be somewhat dark or light colored, with the dark specimens usually shinier as a result of less microtomentum. There is a tendency for *P. obscura* to be darker and shinier and for *P. decipiens* to be lighter and duller but with considerable variation between the two species.

The shapes of the aedeagus and gonites, however, are very distinctive, and readily provide characters to separate the two species. The aedeagus in *P. obscura* (Figs. 32, 33) is narrower from a dorsal view, slightly longer than wide, and the distal end of the sclerotized portion, especially in lateral view, is distinctly pointed. The aedeagus in *P. decipiens* (Figs. 34, 35) is much broader than long in a dorsal view, somewhat rectangular with the distal angles rounded, and in lateral view the distal aspect of the sclerotized portion is slightly concave and with the actual apex of the aedeagus as a pointed process that is extended from an anteroventral angle. Both *P. decipiens* and *P. obscura* occur on St. Vincent and at times were collected in the same swing of an aerial net.

19. *Zeros flavipes* (Williston)

? Ilythea flavipes Williston, 1896:403.
Zeros flavipes.—Cresson, 1943:14 [generic combination].—Wirth, 1968a:18 [neotropical catalog].

Type material.—The lectotype male (designated here) is labeled "Co-type [circular label with a yellow border]/Windward side St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./May/[rectangular gray label]/Ilythea ? flavipes Will [handwritten, two red submarginal borders]/LECTOTYPE Ilythea flavipes Will. ♂ By W.N.Mathis [handwritten except for "LECTOTYPE" and "By", black submarginal border]." The lectotype is deposited in the BMNH. There is also one female paralectotype (BMNH). Williston, in the original description, noted that there were "Two specimens." One female specimen, listed as a syntype (20316, poor condition, head and wings missing) in the AMNH, cannot be considered as one of the primary types since the original series comprised only two specimens.

Other specimens examined from St. Vincent.—St. Andrew Parish: Buccament Bay, 25–28 Mar 1989, W. N. Mathis (1 ♂, 2 ♀; USNM); Camden Park, 25 Mar 1989, W. N. Mathis (4 ♂, 2 ♀; USNM). St. George Parish: Yambou Head, 27 Mar 1989, W. N. Mathis (6 ♂, 5 ♀; USNM).

Distribution.—Afrotropical: Zaire. Nearctic: Canada (ON), USA (FL, OH, TX, WV). Neotropical: Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Mexico, Panama, West Indies (Cuba, Jamaica, Puerto Rico, St. Vincent).

Remarks.—Although *Z. flavipes* is common on St. Vincent, it is not the only species of *Zeros* known to occur there. Two other species, *Z. fenestralis* (Cresson) and *Z. obscurus* (Cresson), are also common, but *Z. flavipes* is easily distinguished from them by the shiny black, mostly bare abdomen. This species may also be distinguished from congeners as follows: vein R2+3 nearly straight, not distinctly undulated; cell R2+3 with three infuscate spots or transverse bars; and crossvein dm-cu present.

20. *Nostima pulchra* (Williston)

Hydrellia pulchra Williston, 1896:399.
Philygria basalis Cresson, 1914:246.—Hendel, 1930:141 [synonymy].
Nostima pulchra.—Hendel, 1930:141 [generic combination].—Cresson, 1938:34 [review]; 1941:6 [review].—Wirth, 1968a: 17 [neotropical catalog].
Nostima (*Nostima*) pulchra.—Cresson, 1947:42 [review].

Type material.—The holotype male of *Hydrellia pulchra* is labeled "Type [circular label with a red border]/St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./May/[a rectangular gray label]/Hydrellia pulchra Will [handwritten, two red submarginal borders]/Nostima pulchra (Williston) ♂ det. WNMathis Edmiston 1991 [species name, gender and "Edmiston" handwritten, black submarginal border]." The holotype is double mounted (pin in a rectangular piece of cardboard), is in good condition (right wing tip and 1st flagellomere of left antenna are missing), and is deposited in the BMNH.

The holotype male of *P. basalis* (Argentina. Tucumán) is deposited in the HNHM.

Distribution.—Neotropical: Argentina, Belize, Brazil, Colombia, Costa Rica, El Salvador, Guatemala, Mexico, Panama, Paraguay, Peru, West Indies (Dominica, Haiti, Puerto Rico, St. Vincent).

Remarks.—This species is distinguished from congeners by the following combination of characters: wing with dark basal band; silvery gray microtomentose spots on abdomen as follows: tergum 2 with posterolateral spot, tergum 3 with band on posterolateral margins not reaching lateral margins dorsomedially, tergum 3 with posterolateral spot; tergum 4 with anterodorsal roughly oval spots and spots posterolaterally, tergum 5 with semicircle area on posteromedial margins.

21. *Nostima willistoni* Wirth

Hydrina nitida Williston, 1896:400 [preoccupied, Robineau-Desvoidy, 1830].

Nostima willistoni Wirth, 1968a:17 [neotropical catalog; replacement name for *H. nitida* Williston].

Type material.—The holotype male is labeled "Type [circular label with a red border]/500 feet./[a pink square label]/St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./Hydrina nitida Will [handwritten, two red submarginal borders/Nostima willistoni Wirth ♂ det. WNMathis Edmiston 1991 [species name, gender and "Edmiston" handwritten, black submarginal border]." The holotype is double mounted (glue covers and obscures most of specimen; right wing, both antennae, most setae, and legs except for coxae 1, 2 and 3, and femur 3 missing), and is deposited in the BMNH.

Distribution.—Neotropical: West Indies (Dominica, St. Vincent).

Remarks.—This species is distinguished from congeners by the following combination of characters: gena with dense microtomentum ventrally; mesonotum vittate; wing veins and crossveins unicolorous; and abdomen shiny brown with microtomentum pattern on abdomen as follows: terga 1–5 with sparse yellowish-silver microtomentum; tergum 4 with silvery gray posterolateral spot along posterior margin.

22. *Hyadina nitifrons* (Williston), new combination

Hydrina nitifrons Williston, 1896:401.

Hydrina nitidifrons [sic].—Cresson, 1947:44 [discussion].

Philygria nitifrons.—Aldrich, 1905:627 [generic combination].—Wirth, 1968a:16 [neotropical catalog].

Type material.—The holotype female (not a male as Williston noted) is labeled "Type [circular label with a red border]/St. Vincent, W.I. H. H. Smith/W. Indies. 1907–66./Hydrina nitifrons Will. [handwritten, two red submarginal borders]/Hyadina nitifrons (Williston) ♀ det. WNMathis Edmiston 1991 [species name, gender and "Edmiston" handwritten, black submarginal border]." The holotype is double mounted (glued to a rectangular piece of cardboard), is in fair condition (antennae and several setae missing), and is deposited in the BMNH.

Other specimens examined from St. Vincent.—St. George Parish: Kingstown, Bo-

tanical Garden, 25-27 Mar 1989, W. N. Mathis (1 ♂; USNM).

Distribution.—Neotropical: West Indies (St. Vincent).

Remarks.—The neotropical species of *Hyadina* are now being revised (Clausen, pers. comm.), and a more extensive diagnosis will be included in that revision. External characters that we have noted to distinguish this species are as follows: parafacial invested with silvery-white microtomentum; anterior margin of notopleuron whitish gray, more densely microtomentose; mesonotum with presutural, prescutellar and supra-alar area of scutum somewhat bare, sparsely microtomentose, subshining, otherwise mesonotum invested with yellowish silver microtomentum; legs yellow, 4th and 5th tarsomeres darker, yellowish brown; wing faintly amber colored, veins and crossvein unicolorous, yellowish brown.

23. *Dagus rostratus* (Cresson)

Ephydra pygmaea Williston, 1896:402 [preoccupied, Haliday, 1833].

Ephydra rostrata Cresson, 1918:66 [replacement name for *E. pygmaea* Williston].

Dagus rostratus.—Wirth, 1968a:24 [neotropical catalog].—Mathis, 1982:21 [lectotype designation]; 1983:720–722 [revision].

Type material.—The lectotype male (designated by Mathis 1982:21) is labeled "Cotype [disk with yellow border]/Windward side St. Vincent, W[est]. I[ndies]. H. H. Smith./W.Indies 1907–66./1000 feet./ Ephydra pygmaea Will [handwritten, two red submarginal borders]/LECTOTYPE ♂ Ephydra pygmaea Williston by W.N. Mathis [handwritten, red]." The lectoytype is double mounted (minute nadel in rectangular piece of cardboard), is in good condition (the first flagellomere of the right antenna is missing), and is in the BMNH. The BMNH also has one male and six female paralectotypes. KU has a male paralectotype, which bears a label with "500 feet." printed on it. AMNH has a male and female paralectotype, which bear "Perseverance Val. 1000 ft." on a locality label. In the original description, Wiliston noted "Fifteen specimens. Perseverance Valley, St. Vincent."

Other specimens examined from St. Vincent.—Charlotte Parish: Montreal, 26 Mar 1989, W. N. Mathis (8 ♂, 1 ♀; USNM). St. Andrew Parish: Camden Park, 25 Mar 1989, W. N. Mathis (7 ♂, 7 ♀; USNM). St. Patrick Parish: Gordon Yard (2 km S Spring Village, 125 m), 11 Jul 1989, M. Sorensson, B. Mårtensson (5 ♂, 7 ♀; ZIL).

Distribution.—Neotropical: Brazil (Cresson, 1935:346), Costa Rica (Cresson, 1918: 66), Guatemala, Mexico, Venezuela, West Indies (Cuba, Dominica, Grenada, Jamaica, Saint Vincent).

Remarks.—Perseverance Valley is one of the few specific localities that Williston noted in his treatment. The specimens collected in the valley have elevational data, which vary from 500 to 1000 ft.

This species is most similar to *D. trichocerus* but is distinguished from it and other congeners by the following combination of characters: face with mostly brown, microtomentose vestiture; dorsocentral setae 3–4 pairs; arista short (slightly more than 2× length of 1st flagellomere) and bearing, short, generally inconspicuous hairs; and epandrium of male trangular, distinctly pointed ventrally.

24. *Scatella obscura* Williston

Scatella obscura Williston, 1896:403.—Wirth, 1968a:26 [neotropical catalog].

Type material.—The lectotype male (designated here) is labeled "Co-type [circular label with a yellow border]/St. Vincent, W.I. H. H. Smith./W.Indies. 1907–66./[brownish pink square label]/Scatella obscura Will [handwritten, two red submarginal borders]/LECTOTYPE Scatella obscura Will. ♂ By W.N.Mathis [handwritten except for

"LECTOTYPE" and "By", black submarginal border]." The lectotype is double mounted (pin in a rectangular piece of cardboard), is in good condition, and is deposited in the BMNH. There are also six paralectotypes as follows: BMNH (3 ♂, 2 ♀, 1?). Williston, in the original description, noted that there were "Eight specimens."

Other specimens examined from St. Vincent.—St. Andrew Parish: Buccament Bay, 25–28 Mar 1989, W. N. Mathis (13 ♂, 9 ♀; USNM); Camden Park, 25 Mar 1989, W. N. Mathis (2 ♀; USNM). St. George Parish: Yambou Head, 27 Mar 1989, W. N. Mathis (7 ♂, 3 ♀; USNM).

Distribution.—Nearctic: USA (FL). Neotropical: Argentina, Brazil, Costa Rica, Ecuador, El Salvador, Panama, Paraguay, West Indies (Bahamas, Dominica, Puerto Rico, St. Vincent).

Remarks.—This species is distinguished from related congeners by the following characters: general coloration brown; mesofrons partially microtomentose, subshiny; gena low, height less than ⅓ eye height; wing infuscate and with several pale spots; both notopleural setae inserted at about same level.

Acknowledgments

For gracious hospitality and allowing access to collections during visits, we thank Roy Danielsson, Museum of Zoology and Entomology, Lund University, Lund, Sweden; James K. Liebherr, Cornell University, Ithaca, New York; David A. Grimaldi, American Museum of Natural History, New York; Brian Pitkin and John Chainey, The Natural History Museum, London, England; and Ian White, Commonwealth Agricultural Bureau International Institute of Entomology (at The Natural History Museum), London, England. We are also grateful to Steve Ashe, The Snow Entomological Collection, The University of Kansas, Lawrence, Kansas, and to David Furth, The Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, for the loan of specimens.

Field work on St. Vincent was supported by a grant from the Research Opportunity Fund, administered by Stanwyn G. Shetler, Acting Deputy Director, USNM.

Susann G. Braden and Vickie Godwin assisted with the scanning electron microscopy, Victor E. Krantz assisted with production of the photographs, and Elaine R. S. Hodges inked the line drawings (except for Figs. 28–31). For critically reviewing a draft of this paper, we thank P. J. Clausen, B. A. Foote, C. W. Sabrosky, W. W. Wirth, and Amnon Freidberg. The latter also accompanied one of us (WNM) on a field trip to St. Vincent in 1989 and collected many shore-fly specimens.

Literature Cited

Adachi, M. S. 1952. New records and name changes in Hawaiian Ephydridae.—Proceedings of the Hawaiian Entomological Society 14(3):353–354.

Aldrich, J. M. 1905. A catalogue of North American Diptera (or two-winged flies).—Smithsonian Institution, Smithsonian Miscellaneous Collections 46(1444):1–680.

Clausen, P. J. 1977. A revision of the nearctic, neotropical, and palearctic species of the genus *Ochthera,* including one Ethiopian species, and one new species from India.—Transactions of the American Entomological Society 103:451–530.

Cogan, B. H. 1980. 71. Family Ephydridae. Pp. 655–669 *in* R. W. Crosskey, ed., Catalogue of the Diptera of the Afrotropical Region, London. British Museum (Natural History), 1437 pp.

Coquillett, D. 1900a. New genera and species of Ephydridae.—The Canadian Entomologist 32(2): 33–36.

———. 1900b. Report on a collection of dipterous insects from Puerto Rico.—Proceedings of the United States National Museum 22:249–270.

———. 1902. New acalyptrate Diptera from North America.—Journal of the New York Entomological Society 10(4):177–191.

Cresson, E. T., Jr. 1914. Descriptions of new genera and species of the dipterous family Ephydridae.—I.—Entomological News 25:241–250.

———. 1916. Descriptions of new genera and species of the dipterous family Ephydridae.—III.—Entomological News 27:147–152.

———. 1917. Studies in the American Ephydridae

(Diptera). II. A revision of the species of the genera *Notiphila* and *Dichaeta*.—Transactions of the American Entomological Society 43:27–66.

———. 1918. Costa Rican Diptera collected by Philip P. Calvert, PH.D., 1909–1910. Paper 3.—A report on the Ephydridae.—Transactions of the American Entomological Society 44:39–68.

———. 1930. Descriptions of new genera and species of the dipterous family Ephydridae. Paper VIII.—Entomological News 41(3):76–81.

———. 1935. Descriptions of new genera and species of the dipterous family Ephydridae.—Transactions of the American Entomological Society 61: 345–372.

———. 1938. Notes on, and descriptions of, some neotropical Ephydridae (Dipt.).—Revista de Entomologa 8(1–2):24–40.

———. 1941. The species of the neotropical genus *Nostima* (Diptera: Ephydridae).—Notulae Naturae 78:1–8.

———. 1942. Synopses of North American Ephydridae (Diptera) I. The subfamily Psilopinae, with descriptions of new species.—Transactions of the American Entomological Society 68:101–128.

———. 1943. The species of the tribe Ilytheini (Diptera: Ephydridae: Notiphilinae).—Transactions of the American Entomological Society 69:1–16.

———. 1944. Descriptions of new genera and species of the dipterous family Ephydridae. Paper XIV. Notulae Naturae.—The Academy of Natural Sciences of Philadelphia 135:1–9.

———. 1946. A systematic annotated arrangement of the genera and species of the neotropical Ephydridae (Diptera). I. The subfamily Psilopinae.—Transactions of the American Entomological Society 71:129–163.

———. 1947. A systematic annotated arrangement of the genera and species of the neotropical Ephydridae (Diptera). II. The subfamily Notiphilinae.—Transactions of the American Entomological Society 73:35–61.

Curran, C. H. 1928. Diptera or two-winged flies. *In* Insects of Porto Rico and the Virgin Islands. *In* C. H. Curran, C. P. Alexander, C. R. Twinn, E. P. van Duzee, eds., Scientific survey of Porto Rico and Virgin Islands.—Annals of the New York Academy of Science 11(1):1–118.

Harrison, A. D., & J. J. Rankin. 1976. Hydrobiological studies of eastern Lesser Antillean Islands. I. St. Vincent: freshwater habitats and water chemistry.—Archiv für Hydrobiologie, Supplement 50:96–144.

Hendel, F. 1930. Die Ausbeute der deutschen Chaco-Expedition 1925/26. Diptera. XIX. Ephydridae.—Konowia 9:127–155.

———. 1936. Ergebnisse einer zoologischen Sammelreise nach Brasilien, insbesondere in das Amazonasgebiet, ausgeführt von Dr. H. Zerny. X. Teil. Diptera: Muscidae acalyptratae (excl. Chloropidae).—Annalen des naturhistorischen Museums in Wien 47:61–106.

Loew, H. 1878. Neue nordamerikanische Ephydrinen.—Zeitschrift für die Gesammten Naturwissenschaften 51:192–203.

Mathis, W. N. 1979. Studies of Notiphilinae (Diptera: Ephydridae), I: revision of the nearctic species of *Notiphila* Fallén, exlcuding the *caudata* group.—Smithsonian Contributions to Zoology 287:1–111.

———. 1982. Studies of Ephydrinae (Diptera: Ephydridae), VI: review of the tribe Dagini.—Smithsonian Contributions to Zoology 345:1–30.

———. 1983. A revision of the genus *Dagus* Cresson (Diptera: Ephydridae).—Proceedings of the Entomological Society of Washington 85:717–726.

———. 1989. 66. Family Ephydridae. Pp. 639–649 *in* N. L. Evenhuis, ed., Catalog of the Diptera of the Australasian and Oceanian regions, E. J. Brill and B. P. Bishop Museum special publication 86, 1155 pp.

———. 1991. Studies of Gymomyzinae (Diptera: Ephydridae), II: A revision of the shore fly subgenus *Pseudohecamede* Hendel of the genus *Allotrichoma* Becker.—Smithsonian Contributions to Zoology 522:1–28.

———. 1992. Family Ephydridae. *In* F. C. Thompson, ed., Checklist of Diptera of America north of Mexico (in press).

Papavero, N. 1973. Essays on the history of neotropical dipterology, with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de Sao Paulo. Vol. II, 446 pp.

Röder, V. von. 1889. *Psilopa (Ephygrobia) Girschneri* n. sp.—Entomologische Nachricten 15(4):54–56.

Sturtevant, A. H. 1923. New species and notes on synonymy and distribution of Muscidae acalypteratae (Diptera).—American Museum Novitates 76:1–12.

———, & M. R. Wheeler. 1954. Synopses of nearctic Ephydridae (Diptera).—Transactions of the American Entomological Society 79:151–257.

Wheeler, W. M. 1896. The genus *Ochthera*.—Entomological News 7:121–123.

Williston, S. W. 1896. XI. On the Diptera of St. Vincent (West Indies).—Transactions of the Entomological Society of London 3:253–446.

———. 1897. Diptera Brasiliana.—Kansas University Quarterly 6(1):1–12.

Wirth, W. W. 1956. The Ephydridae (Diptera) of the Bahama Islands.—American Museum Novitates 1817:1–20.

———. 1965. Family Ephydridae. Pp. 734–759 *in* A. Stone, et al., eds., A catalog of the Diptera of America north of Mexico.—United States Department of Agriculture, Agriculture Handbook, 276:iv + 1696 pp.

———. 1968a. 77. Family Ephydridae. Pp. 1–43 *in* N. Papavero, ed., A catalogue of the Diptera of the Americas south of the United States. Departmento de Zoologia, Secretaria da Agricultura, São Paulo.

———. 1968b. The genus *Typopsilopa* Cresson in the Western Hemisphere.—Proceedings of the Entomological Society of Washington 70(3):225–237.

(WNM) Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.; (JFE) Padua Franciscan Friary, 7022 State Road, Parma, Ohio 44134, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 840–869

EXALLODONTUS AGUANAI, A NEW GENUS AND SPECIES OF PIMELODIDAE (PISCES: SILURIFORMES) FROM DEEP RIVER CHANNELS OF SOUTH AMERICA, AND DELIMITATION OF THE SUBFAMILY PIMELODINAE

John G. Lundberg, Francisco Mago-Leccia, and Pedro Nass

Abstract.—A new genus and species of pimelodid catfish, *Exallodontus aguanai,* is described from the deep channels of the Orinoco and Amazon rivers. This taxon is diagnosed by autapomorphically robust jaw teeth reduced to 2–3 rows, and an obtusely triangular "lacrimal" (=infraorbital 1+2). Also, this taxon has a unique combination of phylogenetically advanced characters—long adipose fin, short dorsal-fin spine, short head, very small eye, vertical neural spines on middle vertebrae, sharply ridged supraoccipital process, paddle-like anterior anal-fin rays, and transversely oriented posterior nares.

The subfamily Pimelodinae is circumscribed to include 32 nominal genera: *Aguarunichthys, Bagropsis, Bergiaria, Brachyplatystoma, Calophysus, Cheirocerus, Conorhynchos, Duopalatinus, Exallodontus, Goslinia, Hemisorubim, Hypophthalmus, Iheringichthys, Leiarius, Luciopimelodus, Megalonema, Merodontodus, Perrunichthys, Parapimelodus, Paulicea, Phractocephalus, Pimelodina, Pimelodus, Pinirampus, Piramutana, Platynematichthys, Platysilurus, Platystomatichthys, Pseudoplatystoma, Sorubim, Sorubimichthys,* and *Steindachneridion.* This subfamily is supported by three synapomorphic characters—the dendritic arrangement of lateral line system on the head and nape, an elongated lateral ethmoid-palatine condyle, and a sutural joint between the fifth and sixth centra. Within the Pimelodinae three nested subgroups are delineated and diagnosed but not named formally: (1) "Group A," comprising all pimelodines except *Phractocephalus, Leiarius* and *Perrunichthys*; (2) "*Calophysus-Pimelodus* clade" that includes Stewart's (1986a) "*Calophysus* group" (*Calophysus, Pinirampus, Pimelodina, Luciopimelodus* and *Aguarunichthys*) plus *Megalonema* plus our third group; (3) "*Pimelodus* group" composed of the nominal genera *Bagropsis, Bergiaria, Cheirocerus, Conorhynchos, Duopalatinus, Exallodontus, Iheringichthys, Parapimelodus, Pimelodus, Platysilurus,* and *Platystomatichthys.* Variations of the trigeminofacial nerve foramina are described in relation to a possible phylogenetic diagnosis of *Pimelodus.*

Resumen.—En este trabajo se describe a *Exallodontus aguanai,* un nuevo género y nueva especie de bagre pimelódido proveniente de los canales profundos de los ríos Orinoco y Amazon. *Exallodontus* se reconoce por dos carácteres autapomórficos: (1) dientes mandibulares robustos y reducidos a 2 ó 3 filas, y (2) presencia de un lacrimal (infraorbitario 1+2) triangular con ángulos obtusos. Este taxon tiene, además, una combinación única de carácteres filogeneticamente avanzados—aleta adiposa larga, espina de la aleta dorsal corta, cabeza relativamente pequeña, ojo muy pequeño, espinas neurales verticales en las vértebras localizadas hacia la mitad de la columna, processo

supraoccipital con una cresta pronunciada, radios anales anteriores en forma de paleta, y narceas posteriores orientadas transversalmente.

La subfamilia Pimelodinae se ha restringido para incluir los siguientes 32 géneros nominales: *Aguarunichthys, Bagropsis, Bergiaria, Brachyplatystoma, Calophysus, Cheirocerus, Conorhynchos, Duopalatinus, Exallodontus, Goslinia, Hemisorubim, Hypophthalmus, Iheringichthys, Leiarius, Luciopimelodus, Megalonema, Merodontodus, Perrunichthys, Parapimelodus, Paulicea, Phractocephalus, Pimelodina, Pimelodus, Pinirampus, Piramutana, Platynematichthys, Platysilurus, Platystomatichthys, Pseudoplatystoma, Sorubim, Sorubimichthys,* y *Steindachneridion.* Esta subfamilia esta definida por tres caráctares sinapomórficos—organización dendrítica de los canales del sistema de la línea lateral en la cabeza y la nuca, cóndilo palatino del etmoides lateral alargado, y una unión sutural entre los centra de la 5a. y 6a. vértebras. Entre los Pimelodinae se delimitan tres subgrupos o clados que son aquí definidos, pero a los cuales no se les asigna ningún nombre formal: (1) "Grupo A," que abarca a todos los Pimelodinae con la excepción de *Phractocephalus, Leiarius* y *Perrunichthys*; (2) un "clado *Calophysus-Pimelodus*" que incluye el "grupo *Calophysus*" de Stewart (1986a), es decir, *Calophysus, Pinirampus, Pimelodina, Luciopimelodus* y *Aguarunichthys,* más *Megalonema* y nuestro tercer grupo, (3) un "grupo *Pimelodus*" formado por los géneros nominales *Bagropsis, Bergiaria, Cheirocerus, Conorhynchos, Duopalatinus, Exallodontus, Iheringichthys, Parapimelodus, Pimelodus, Platysilurus,* y *Platystomatichthys.* Finalmente, se describen las variaciones de los forámenes del nervio trigéminofacial en relación con una posible diagnosis filogenética de *Pimelodus.*

During the Catherwood Foundation Peruvian-Amazon Expedition in 1955, personnel from the Academy of Natural Sciences of Philadelphia made a collection of fishes in the Río Marañón using a small trawl. Böhlke (1970:2) reported that this collection contained some unusual catfishes and he urged "that more bottom sampling should be attempted in the large South American rivers." Later, in 1978 and '79, bottom trawling operations from R/V *Eastward* and smaller craft in the deep river channels of the lower Orinoco yielded a surprising diversity and biomass of fishes (López et al., 1985). These achievements stimulated the use of bottom trawls in other large Neotropical rivers in Venezuela, Colombia, Brazil, Panama and Ecuador. The most significant result of these efforts has been the discovery of an abundance of catfishes and electric fishes in the deep channels, with many distinctive species apparently restricted to this habitat (Mago-Leccia et al. 1985; Lundberg & Stager 1985; Lundberg & Mago-Leccia 1986; Stewart 1985, 1986b). In this paper we describe a distinctive pimelodid catfish that is known only from deep trawl samples—*Exallodontus aguanai.*

In treating the interrelationships of *Exallodontus* we reconsidered some higher level groups of pimelodid catfishes. Recently, a few well-characterized monophyletic groups of pimelodid species and genera have been delimited (Stewart 1986a, Lundberg & McDade 1986, Lundberg et al. 1988, Ferraris 1988). Two pimelodid subfamilies, Rhamdiinae and Pseudopimelodinae, have been diagnosed within an explicit phylogenetic framework (Lundberg et al. 1991). From these alignments of genera it has been possible to more precisely diagnose and re-

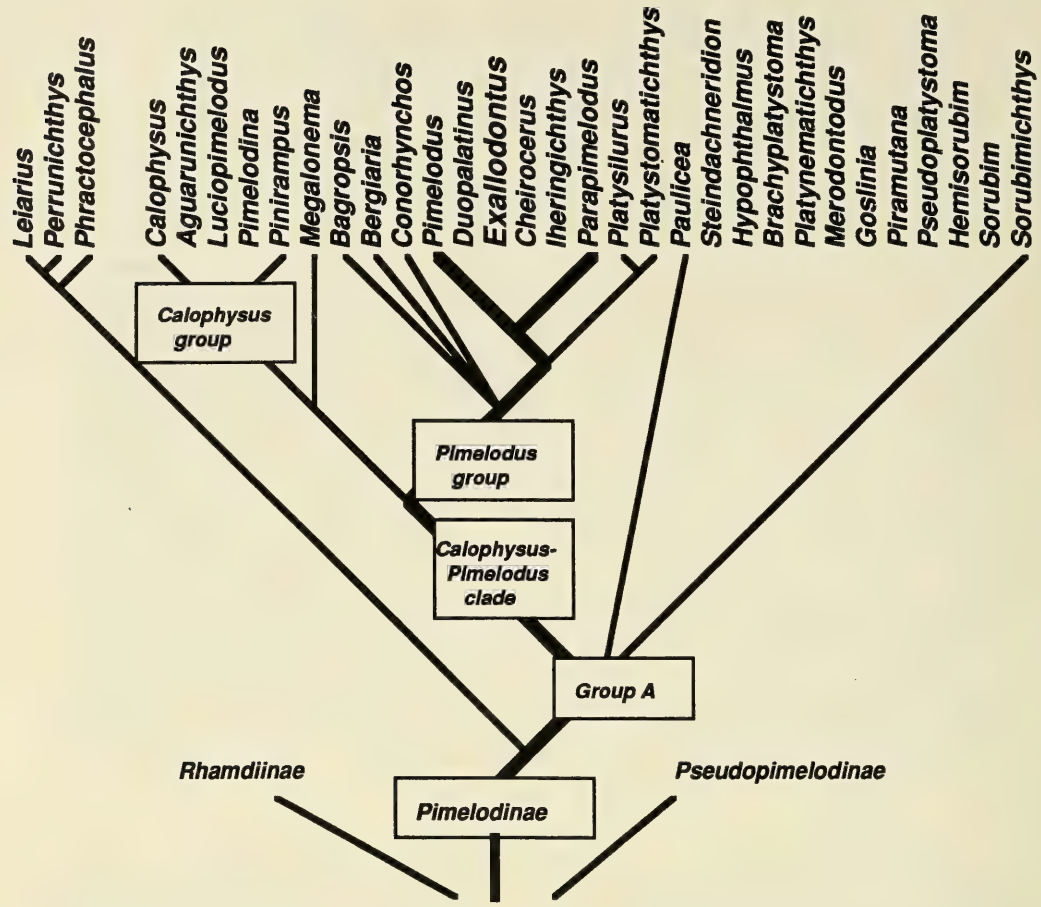


Fig. 1. Diagram of phylogenetic interrelationships of pimelodine catfishes and informal subgroup names used in this paper. Bold lines highlight the higher clades to which *Exallodontus* belongs.

strict the membership of the heretofore vague subfamily Pimelodinae (see Fig. 1 and below).

Methods.—Counts and measurements are those described by Lundberg & McDade (1986). In addition, prepectoral-fin length is the distance from snout tip to base of pectoral spine, and interocular distance is the least distance between dorsal margins of fleshy orbital rims. All measurements are straight-line made with dial calipers held directly on the fish. Measurements and counts in the tables are those for both sexes combined. Measurements in materials list are standard lengths in mm, unless noted otherwise. Gill rakers, branchiostegal rays and vertebrae were enumerated on cleared and stained specimens, dry skeletons and radiographs. Total vertebral counts include five for the Weberian complex and one for the compound caudal centrum (fused preural centrum 1 + ural centra). The first caudal vertebra is the most anterior one with a full hemal spine that is subequal in length to the following spine.

Institutional abbreviations follow Leviton et al. (1985).

In phylogenetic analysis, polarization of character transformation series into primitive (plesiomorphic) and derived (apomorphic) conditions is based on outgroup comparisons to other pimelodid groups (see Comparative pimelodid material examined) following the partly resolved hypoth-

esis shown in Fig. 1 (Lundberg & McDade 1986; Lundberg et al. 1988, 1991), plus other catfish groups (see Comparative non-pimelodid materials examined) with the Diplomystidae and the fossil †Hypsidoridae taken stepwise more inclusively as the sister groups to other catfishes (Grande 1987).

Exallodontus, new genus
Figs. 2–10, 13, Tables 1–3

Type species.—*Exallodontus aguanai,* new species.

Diagnosis.—A genus of catfishes distinguished from other Pimelodidae by two uniquely derived features: (1) 2–3 rows of heavy, firmly attached conical teeth on premaxillae and dentaries (Fig. 2); (2) "lacrimal" (=infraorbital 1+2 in this and other Pimelodinae, see below) shaped as an obtuse-angled triangle with nearly straight sides (Fig. 3).

Exallodontus is further distinguished from other pimelodid genera by having a unique combination of features whose phylogenetic generality is not yet fully determined. These features are useful for identifying the new taxon and will be of value in future comparative studies of the family. These are: (3) relatively long, nearly straight-margined adipose fin (adipose fin length contained 2.0–2.5 in SL, Fig. 5); (4) short dorsal fin spine and low dorsal fin (dorsal-fin spine length contained 5.6–8.6 in SL, Fig. 5); (5) relatively small head (head length contained 4.0–5.2 times in SL, Fig. 5); (6) a relatively small eye (horizontal eye diameter contained 3.4–5.5 times in snout length, 7.4–12.0 times in head length, Fig. 5); (7) neural spines of vertebrae 13 (or 14) to 23 (or 24) oriented 90° to horizontal axis of centra (Fig. 4); (8) supraoccipital process with a narrow median keel above somewhat concave sides (Fig. 6A), markedly angular in cross-section, slender and tapering to its peg-and-socket joint with supraneural (basal width of supraoccipital process about 2 times in length); (9) anterior anal-fin rays broadened, forming a paddle-like blade (Fig. 7); (10) posterior nostril ovoid, with its long axis oriented transversely (Fig. 7).

Comparison.—The foregoing diagnostic features of *Exallodontus* are here compared to similar pimelodid taxa.

1. Dentition of jaw bones (Fig. 2): Generally in catfishes, including most pimelodids, the jaw teeth are in bands with many more than three irregular rows (e.g., Lundberg & McDade 1985:figs. 6, 9), and the teeth are slender, conical, and at least slightly depressible. There are a few pimelodids, however, that have, like *Exallodontus,* a reduced number of tooth rows, but in each case the shape or arrangement of the teeth is very different. *Calophysus macropterus* has two rows of teeth on the premaxillae and a single row on the lower jaw. The outer premaxillary and dentary teeth of *Calophysus* are uniquely incisiform with minutely scalloped edges, and their spacing is highly regular. *Pimelodina flavipinnis* has one or a few rows of weakly attached, very fine teeth on the jaw bones (Stewart 1986a:fig. 1c). *Cheirocerus* (Stewart & Pavlik 1985:fig. 2) and *Iheringichthys* spp. may have single rows or small patches of weak premaxillary teeth in young that are lost with growth, and a single row on the lower jaw. Except for *Calophysus,* the dental conditions of these pimelodids seem clearly to be reductive, unlike the much heavier dentition of *Exallodontus.* The conditions possessed by *Pimelodina, Cheirocerus, Iheringichthys* and *Calophysus* are clearly apomorphic among pimelodids, but the striking differences between them and *Exallodontus* suggest that they are not homologous.

In respect to tooth shape and attachment, we have found that *Pimelodus altissimus* have jaw teeth that are nearly as strongly developed and firmly anchored as those of *Exallodontus,* but *P. altissimus* has 6–8 premaxillary and dentary tooth rows. The similarity between these two species in tooth shape is possibly a synapomorphy.

2. Shape of anteriormost infraorbital or "lacrimal" bone (Fig. 3): The anteriormost infraorbital bone in *Exallodontus* and many

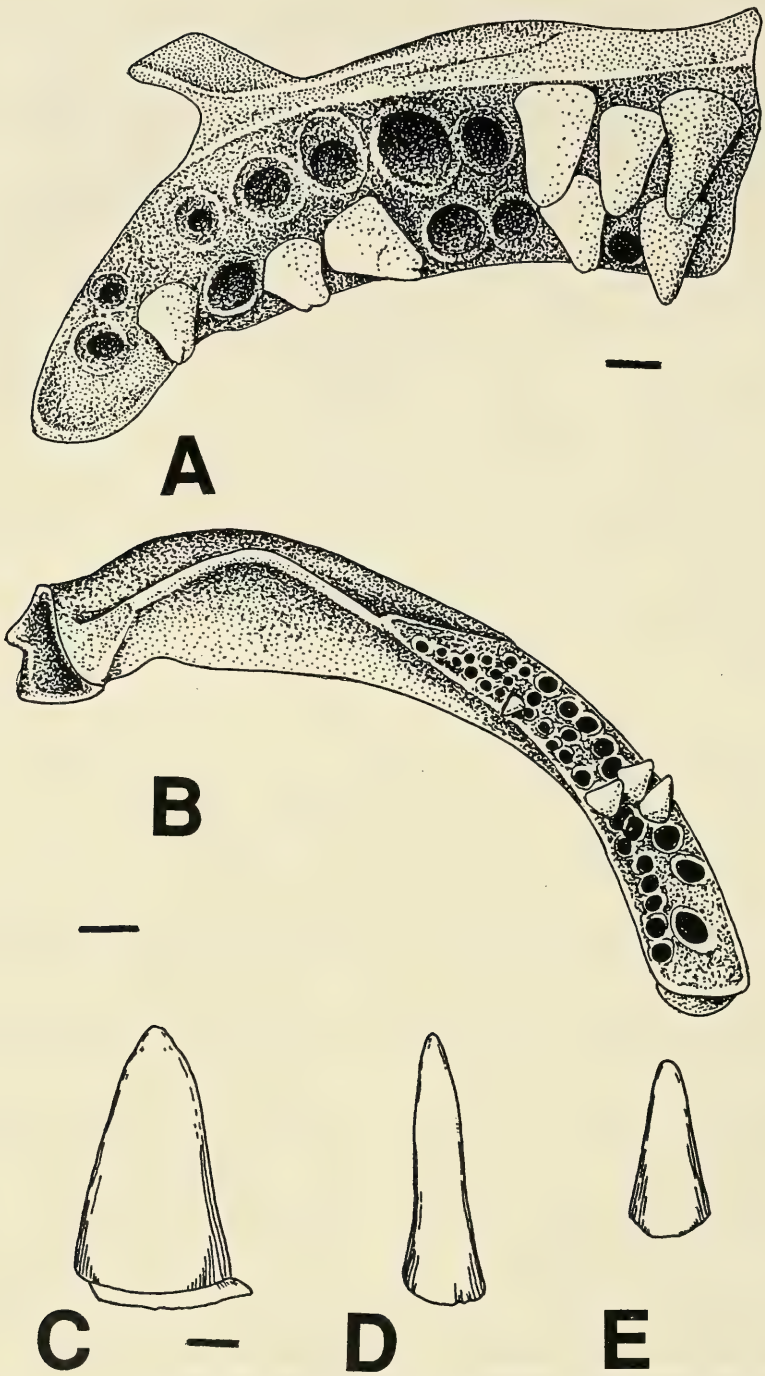


Fig. 2. Jaw bones and dentition of *E. aguanai.* A. Right premaxilla in ventral view, MBUCV-V-ES112, B. Left dentary in dorsal view, MBUCV-V-ES112, C–E. Middle outer row, dentary teeth from comparably sized specimens of C. *E. aguanai,* DU-F-977, 166 mm SL, D. *Pimelodus grosskopfi,* DU-F-919, 211 mm SL, E. *Pimelodus altissimus,* AMNH 40138, 121 mm SL. Scale bars for A = 1 mm, B = 0.5 mm. Single scale bar for C–E = 0.25 mm.

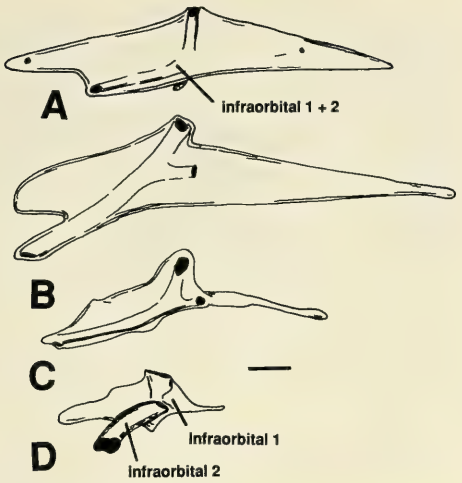


Fig. 3. Right lateral views of infraorbital bones 1 (=lacrimal) and 2 of: A. *E. aguanai.* DU-F-977, B. "*Pimelodus* A" from the Orinoco DU-F-1006, C. *P. pictus,* DU-F-1012, D. *Pimelodella chagresi,* USNM uncat. (Field No. WCS1530, Panama). Single scale bar for A–C = 0.5 mm, for D = 1.0 mm.

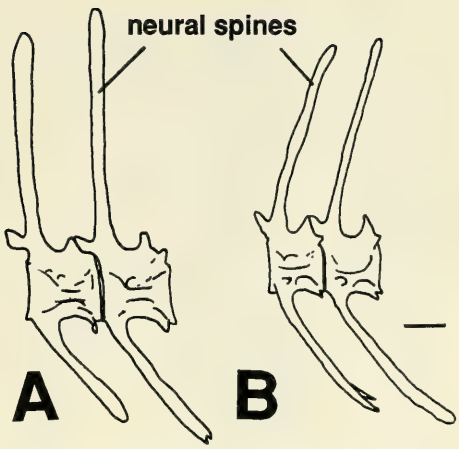


Fig. 4. Left lateral views of mid-body vertebrae of A. *E. aguanai,* vertebrae 16 and 17, DU-F-977, B. *Pimelodus grosskopfi,* vertebrae 17 and 18, DU-F-919. Scale bar = 2.0 mm.

other pimelodids is compound because of fusion between the first and second infraorbital. In most other catfishes, including the "rhamdiine" pimelodids (Lundberg et al. 1991), the second infraorbital is a small, tubular lateralis ossicle that lies laterally adjacent to the posteroventral corner of the first (Fig. 3; see also Lundberg & McDade 1985:fig. 7). Both the compound infraorbital and the separate first and second infraorbitals primitively have a tetraradiate form: anterior and posterior processes of the first infraorbital lie along the margin of the olfactory capsule between the premaxilla and lateral ethmoid, a dorsal process continues the tubular lateralis component that traverses the first infraorbital, and the second infraorbital projects posteroventrally. Uniquely, in *Exallodontus* additional ossification between the four processes creates the triangular and nearly straight-edged form of this bone.

3–6. Morphometric characters: Compared to other generally similar pimelodids *Exallodontus* possesses a relatively small eye and head, low dorsal fin and long adipose fin (Fig. 5).

7. Angle of neural spines (Fig. 4): With only slight variation, in *Exallodontus* the neural spines of vertebrae 13 or 14 to 23 or 24 are oriented at 90° to the horizontal axes of their centra. Vertically oriented neural spines on the mid-body vertebrae are also present in an undescribed Orinocan species that we informally refer to as "*Pimelodus* A." (In Eigenmann & Eigenmann [1890] "*Pimelodus* A" keys to the Amazonian *Pimelodus altipinnis* Steindachner, from which it is clearly different. Furthermore, Mees [1974] has identified the holotype of *altipinnis* as *Pimelodella cristata.* The names and relationships of these *Pimelodus*-like species are under study by D. J. Stewart.) Primitively in catfishes, and probably in most groups of fishes, the neural spines of the posterior precaudal and anterior caudal vertebrae angle at much less than 90% or curve posterodorsally from their centra.

8. Supraoccipital process: In *Exallodontus* the supraoccipital process (Fig. 6A) has a narrow and sharply-angular median ridge, below which the process sides have a slightly concave surface. Generally in catfishes, including pimelodids, that have a supraoc-

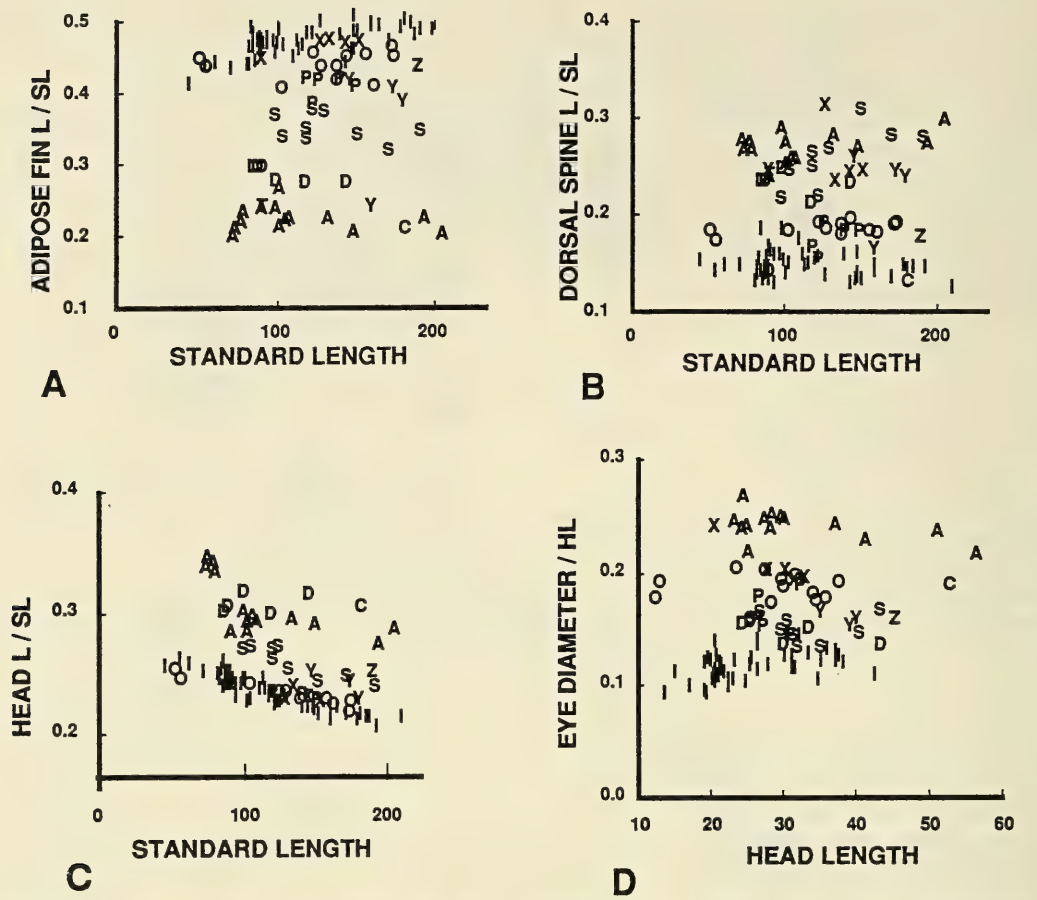


Fig. 5. Scatter plots of A. adipose fin length, B. dorsal spine length, C. head length, and D. eye diameter (expressed as ratios standard length or head length) for *Exallodontus aguanai* and similar pimelodine catfishes. Code to symbols: I = *E. aguanai*, A = *Pimelodus blochi*, C = *Duopalatinus emarginatus*, D = *Duopalatinus peruanus*, O = "*Pimelodus* A" from the Orinoco, P = "*Pimelodus* cf. A" from the Amazon, S = *Pimelodus altissimus*, X = *Pimelodina flavipinnis*, Y = *Calophysus macropterus*, Z = *Pinirampus pirinampu*.

cipital process, it is smoothly convex to flat. There are a few pimelodids, however, that have ridged supraoccipital processes: *Pimelodus altissimus* and *Duopalatinus peruanus*.

9. Anal-fin rays: Large specimens of *Exallodontus* have a paddle-like structure developed from thickened, elongated anterior fin rays. A similar but more hypertrophied structure is found in the undescribed species "*Pimelodus* A" from the Orinoco. Other pimelodids and most other catfishes lack such modified anal-fin rays.

10. Posterior nostril: Nearly all pimelodids and other catfishes have an oval-shaped posterior nostril with its long axis oblique to the longitudinal body axis. *Exallodontus* similarly has an ovoid posterior nostril but its long axis is transverse (Fig. 7B). Among pimelodids a transverse orientation of the posterior nostril has been observed in *Leiarius, Calophysus, Pimelodina* and *Pinirampus*.

In the literature (Eigenmann & Allen 1942, Mees 1974) *Exallodontus* would be identified as a *Pimelodus*. However, three points justify description of *Exallodontus* as a new genus. First, this taxon is readily diagnosed

by uniquely autapomorphic features that mark it as a distinct lineage among the Pimelodidae. *Exallodontus* also has a unique combination of other features, some of which appear to be derived among pimelodids and eventually may be found to be additional autapomorphies of *Exallodontus* within a restricted subgroup of pimelodids, or synapomorphies shared with some other pimelodids. Second, because the sister group of *E. aguanai* is uncertain, we cannot assign this species to *Pimelodus* or another genus without risk of creating a nonmonophyletic group. Third, assignment of *E. aguanai* to *Pimelodus* would radically expand the limits of variation of an already vaguely diagnosed genus. Comparisons of *E. aguanai* and its phylogenetic position among pimelodids are discussed below.

Etymology.—*Exallodontus* from the Greek "exallos" for quite different, and "odontos" for tooth. This is in reference to the unique form of the teeth. The gender is masculine.

Exallodontus aguanai, new species
Figs. 2–10, 13, Tables 1–3

Holotype.—MBUCV-V-18930, 207.0 mm, Venezuela, Territorio Federal Delta Amacuro, Río Orinoco near Los Castillos, 159 n mi from sea buoy at the terminus of the ship navigation channel in Boca Grande, 8°32′N, 62°23′W, 10 Nov 1979, collected by R/V *Eastward* with a 9 m bottom trawl at a depth of 20–30 m.

Paratypes.—Venezuela: Apure State. ANSP 160185, 1, Río Meta upstream from confluence with Río Orinoco, ca. 6°18′N, 67°37′W, 27 Nov 1985, collected by B. Chernoff, W. Saul. MBUCV-V-15017, 1, 85.5 mm, Caño Bucaral, near mouth of Río Arauca, 7°20′N, 66°50′W, 9 Aug 1984, collected by O. Castillo, O. Brull, P. Nass. MBUCV-V-13072, 1, 165 mm, Río Apure in front of San Fernando de Apure, 7°55′N, 67°30′W, 14 Aug 1980, collected by O. Castillo, F. Provenzano. MBUCV-V-15381, 7,

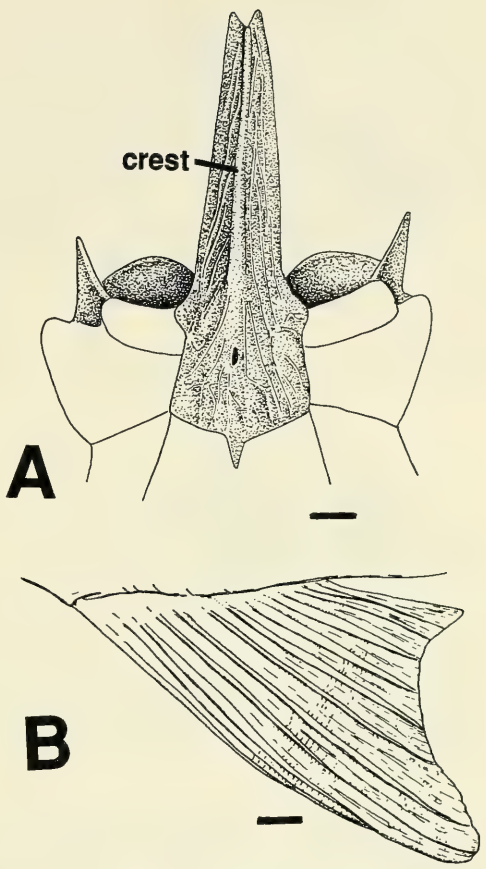


Fig. 6. A. Supraoccipital bone of *Exallodontus aguanai,* MBUCV-V-ES112. B. Anal fin, left side in lateral view, of *Exallodontus aguanai,* to show elongated anterior fin rays, Paratype ANSP 165813, mature specimen 149 mm SL from Río Orinoco, Venezuela. Scale bar for A = 2 mm, scale bar for B = 3 mm.

Río Apure at San Fernando de Apure, 7°55′N, 67°30′W. MBUCV-V-19055, 2, 32–123 mm, Río Apure in front of Laguna Jarina, near San Fernando de Apure, 7°55′N, 67°30′W, 21 May 1983, collected by F. Provenzano. MBUCV-V-19053, 2, 164–164 mm, Río Apure near mouth of Río Portuguesa, 7°55′N, 67°35′W, 22 May 1983, collected by F. Provenzano. MBUCV-V-19054, 2, 75–163 mm, Río Apure near mouth of Río Portuguesa, 7°55′N, 67°35′W, 27 Jul 1983, collected by F. Provenzano. MBUCV-V-19056, 3, 165–199 mm, Río Apure in front of Laguna Jarina, near San Fernando

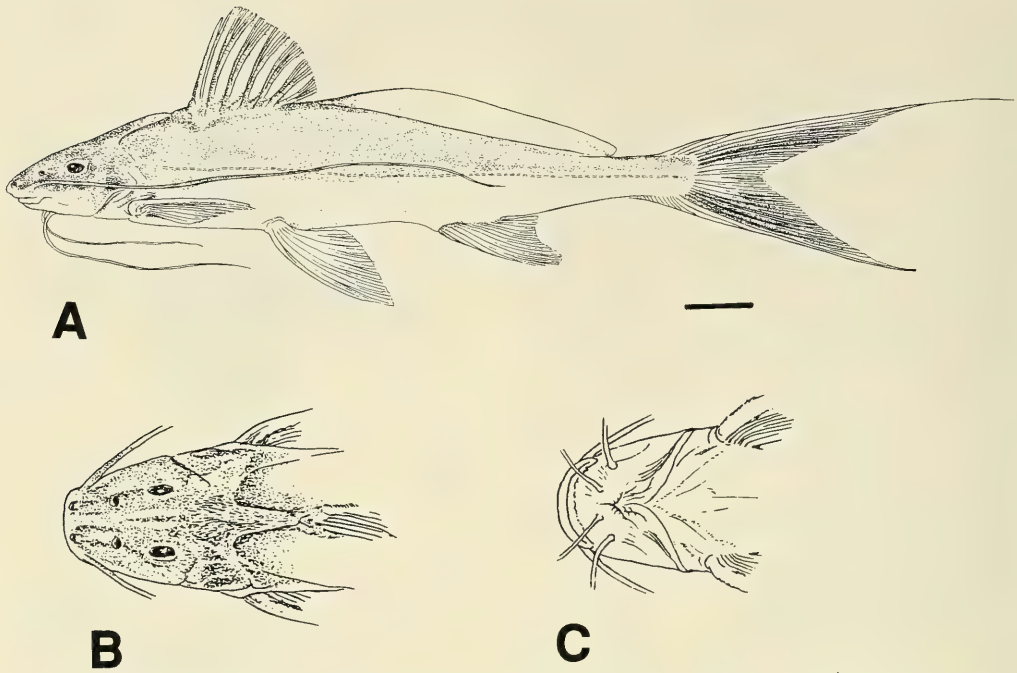


Fig. 7. *Exallodontus aguanai,* Paratype MBUCV-V-11012, mature specimen 175 mm SL from Río Orinoco, Venezuela, A. Left side lateral view, B and C. dorsal and ventral views of head. Single scale bar for A = 15 mm, for B, C = 20 mm.

de Apure, 7°55′N, 67°30′W, 18 Jun 1983, collected by F. Provenzano. MBUCV-V-19057, 4, 68–84 mm, Río Apure in front of airport at San Fernando de Apure, 7°55′N, 67°30′W, 12 Aug 1982, collected by F. Provenzano. MBUCV-V-19058, 5, 123–140 mm, Río Apure in front of Isla Apurito, near San Fernando de Apure, 7°55′N, 67°30′W, 25 Jan 1985, collected by O. Castillo, F. Provenzano. Bolívar State (all collected by R/V *Eastward* in Río Orinoco). BMNH 1990.4.23:2–3, 2, 97–99 mm, 202 n mi from sea buoy, 8°18′N, 65° 56′W, 7 Nov 1979, field number T-9-79. CAS 63850,

Fig. 8. *Exallodontus aguanai,* Paratype ANSP 15077, subadult from Peru, 91.5 mm SL. (Pectoral fin is unnaturally supinated.) Drawn by Ms. G. K. Jensen under the direction of Dr. J. Böhlke.

2, 100–128 mm, 203 n mi from sea buoy, 8°21′N, 62°57′W, 7 Nov 1979, Field number T-11-79. Territorio Federal Delta Amacuro (all collected by R/V *Eastward* in Río Orinoco). AMNH 59041, 3, 113–118mm, near Los Castillos, 160 n mi from sea buoy, 8°32′N, 62°24′W, 10 Nov 1979, field number T-23-79. ANSP 165812, 5, 89–123 mm, near mouth of Caño Tortola, 137 n mi from sea buoy, 8°42′N, 62°05′W, 12 Nov 1979, collected by R/V *Eastward*, field number T-43-79. ANSP 165813, 2, 149–180 mm, 2 km below Barrancas, 140 n mi from sea buoy, 8°44′N, 62°07′W, 17 Feb 1978, collected by R/V *Eastward*, field number JGL-16-78. ANSP 165814, 1, 158 mm, near Isla Veradero downstream from Barrancas, 141 n mi from sea buoy, 8°43′N, 62°08′W, 17 Feb 1978, field number JNB-26-78. DU-F-977, 4, incl. a dry skeleton, 159-180 mm, upstream from El Consejo, 135 n mi from sea buoy, 8°42′N, 62°04′W, 19 Feb 1978, field number JNB-44-78. DU-F-865, 5, incl. 1 cleared and stained, 82–94 mm, near mouth of Caño Tortola, 137 n mi from sea buoy, 8°42′N, 62°05′W, 12 Nov 1979, field number T-45-79. FMNH 99441, 4, 92–111 mm, near mouth of Caño Guine, downstream from El Consejo, 133 n mi from sea buoy, 8°40′N, 62°02′W, 13 Nov 1979, field number T-50-79. FMNH 99442, 3, 119–163 mm, near Barrancas, 141 n mi from sea buoy, 8°42′N, 62°10′W, 12 Nov 1979, field number T-39-79. MBUCV-V-11012, 2, 156–175 mm, near El Consejo, about 136 n mi from sea buoy, 8°42′N, 62°05′W, 19 Feb 1978. MBUCV-V-13734, 1, 190 mm, Isla Portuguesa, 16 Nov 1979. MZUSP 41395, 1, 118 mm, downstream from El Consejo, 130 n mi from sea buoy, 8°40′N, 62°00′W, 14 Nov 1979, field number T-56-79. UMMZ 217309, 2, 78–119 mm, near Caño Araguaito, 130 n mi from sea buoy, 8°40′N, 61°59′W, 22 Nov 1979, field number HLR-42-79. USNM 308421, 1, 188 mm, N side of Isla Tres Caños near mouth of Caño Araguaito, 130 n mi from sea buoy, 8°40′N, 61°59′W, 19 Feb 1978, field number JNB-37-78. USNM 308422, 1, 93 mm, near Los Castillos, 161 n mi from sea buoy, 8°31′N, 62°25′W, 10 Nov 1979, field number T-22-79. USNM 308423, 7, 74–115 mm, near mouth of Caño Guine downstream from El Consejo, 133 n mi from sea buoy, 8°40′N 62°02′W, 13 Nov 1979, field number T-54-79. USNM 320097, 1, 124 mm, near Puerto Cabrian, 151 n mi from sea buoy, 8°35′N, 62°16′W, 11 Nov 1979, field number T-35-79. Monagas State (all collected by R/V *Eastward* in Río Orinoco). LACM 43311-1, 2, 85–111 mm, near Caño los Cocos, across from Los Castillos, 162 n mi from sea buoy, 8°32′N, 62°25′W, 10 Nov 1979, field number HLR-13–79. MBUCV-V-10661, 1, 127 mm, near Barrancas, between N coast and Isla Veradero, ca. 141 n mile from sea buoy, 8°42′N, 62°10′W, 17 Feb 1978. MBUCV-V-13961, 1, 177 mm, collected near Barrancas, between N coast and Isla Veradero, ca. 141 n mile from sea buoy, 8°42′N, 62°10′W, 17 Feb 1978.

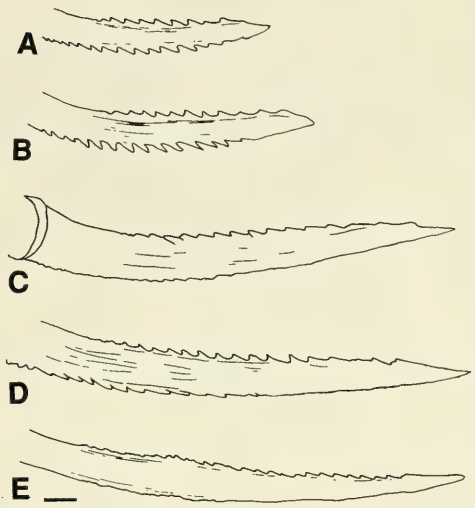


Fig. 9. Dorsal views of left pectoral spines of *Exallodontus aguanai* illustrating negative allometry of dentations. A. Venezuelan specimen 46.9 mm SL, MBUCV-V-19059, B. Peruvian specimen 59.5 mm SL, ANSP 150178, C. Venezuelan specimen 82.5 mm SL, DU-F-1048, D. Peruvian specimen 91.5 mm SL, ANSP 150177, E. Venezuelan specimen, 199.4 mm SL, MBUCV-V-11012. Single scale bar for A and D = 1 mm; for E = 2 mm.

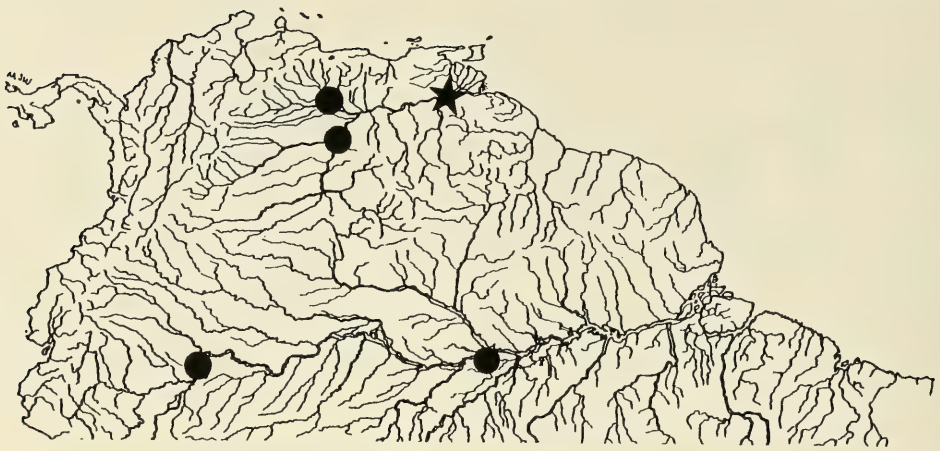


Fig. 10. Geographic distribution of *Exallodontus aguanai* in the Orinoco and Amazon basins. Star = type locality; some symbols represent more than one lot of specimens, see text under Distribution.

Peru: Loreto Department. ANSP 150177, 91.5 mm, and ANSP 150178, 59.5 mm, both from vicinity of Iquitos, Río Amazonas (Marañón) between Isla Iquitos and Isla Lapuna, near Isla Lapuna shore; to 3.66 m in trawl net, 3°51′S, 73°13′W, 9 Oct 1955, collected by C. C. G. Chaplin and R. Patrick.

Brazil: Amazonas. INPA 4450, 1, 140 mm, Rio Amazonas 2–3 km downstream of Manaus, collected with 3 m try net trawl in channels ca. 20–40 m, 3°40′S, 59°40′W, Nov 1990, collected by J. Lundberg, L. Py-Daniel, N. L. Chao, and C. Cox Fernandes. INPA 4451, 2, 47–64 mm, Rio Solimões, 5 km upstream of Manaus with 3 m try net trawl in channels ca. 20–40 m, 3°10′S, 60°20′W, Dec 1990, collected by J. Lundberg, L. Py-Daniel, N. L. Chao, and C. Cox Fernandes.

Non-type specimens examined.—Venezuela: Apure State. MBUCV-V-19059, 4 cleared and stained, 48–61 mm, Río Apure in front of Boquerones near San Fernando de Apure, 7°55′N, 67°30′W, collected by F. Provenzano. Bolívar State (all collected by R/V *Eastward* in Río Orinoco). DU-F-1024, 1, 145 mm, near Ciudad Bolivar, 241 n mi from sea buoy, 8°09′N, 63°32′W, 9 Nov 1979, field number ECM-2-79. DU-F-1025, 1, 88 mm, near San Felix S of Isla Fajardo, 180 n mi from sea buoy, 8°22′N, 62°40′W, 6 Nov 1979, field number T-1-79. DU-F-1026, 1, 90 mm, 202 n mi from sea buoy, 8°18′N, 65°56′W, 7 Nov 1979, field number T-10-79. DU-F-1027, 1, 90 mm, 201 n mi from sea buoy, 8°18′N, 62°56′W, 8 Nov

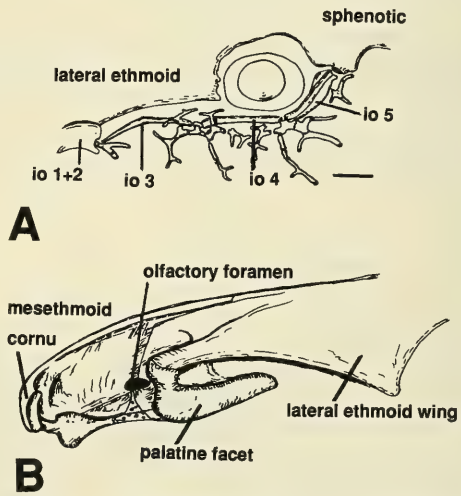


Fig. 11. A. Dendritic arrangement of lateral line tubes as exemplified by infraorbital region of *Pimelodus altissimus*, AMNH 40138. B. Elongated palatine facet on the lateral ethmoid as exemplified by *Pimelodus grosskopfi*, DU-F-919. Single scale bar for both = 2 mm.

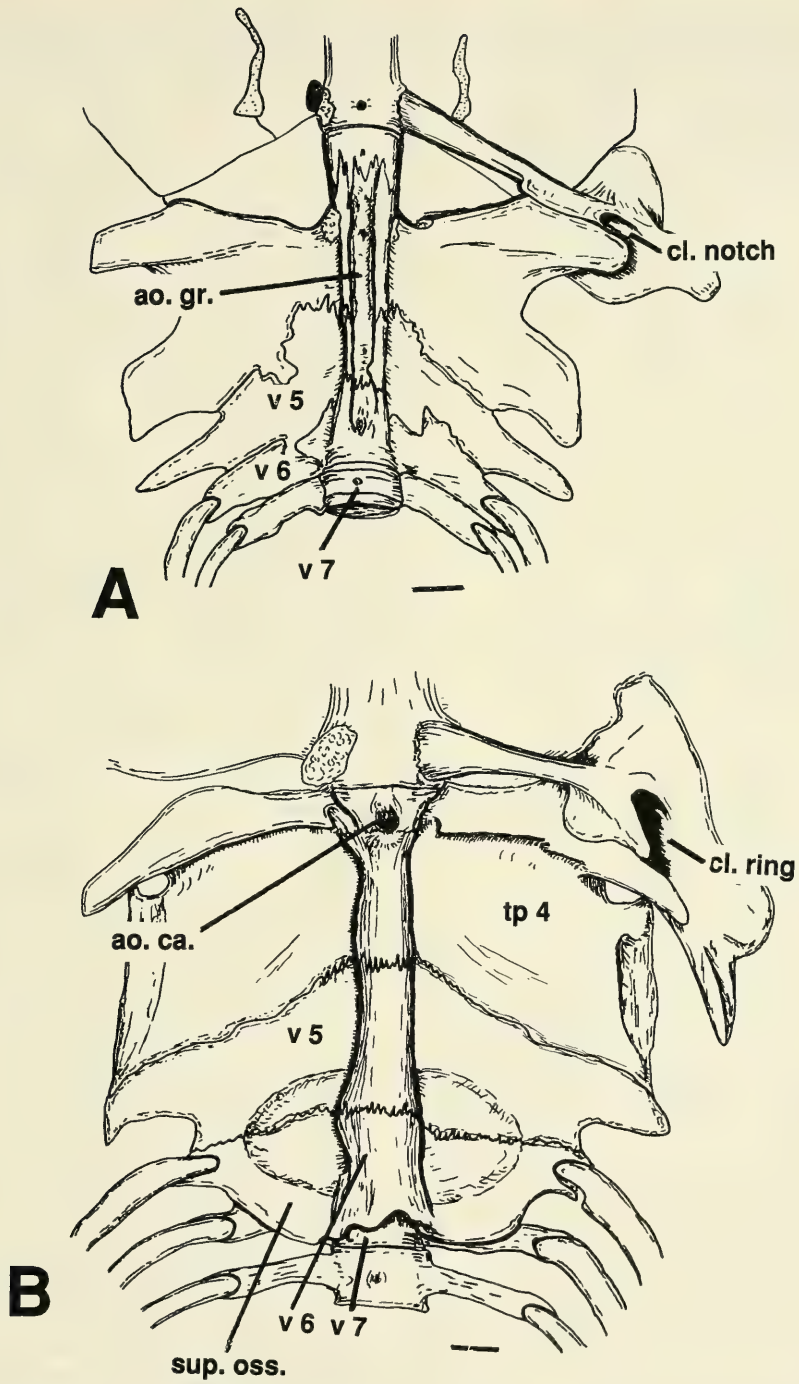


Fig. 12. Weberian complex, basioccipital region and upper part of shoulder girdle of A. *Phractocephalus hemiliopterus,* DU-F-925, and B. *Pimelodus grosskopfi,* DU-F-919, Scale bar for A = 5 mm, for B = 2 mm. ao. ca. = aortic canal; ao. gr. = aortic groove; cl. notch = notch for cleithrum in supracleithrum; cl. ring = "cleithral ring"; sup. oss. = superficial ossification on vertebral centra; tp4 = transverse process of vertebra 4; V5, V6, V7 = vertebrae with their ordinal numbers.

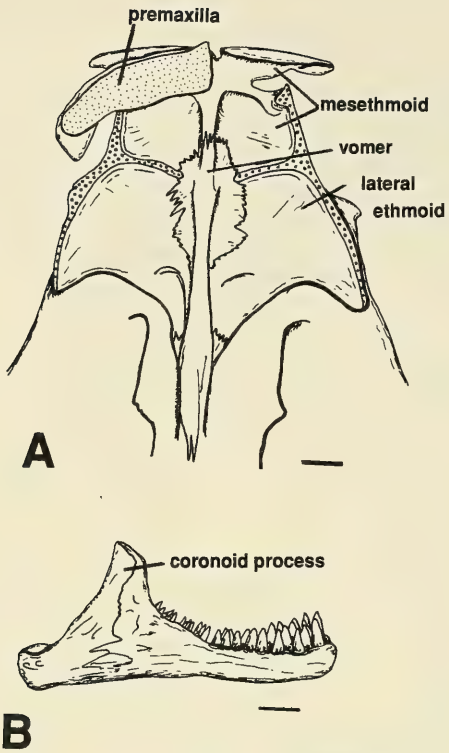


Fig. 13. A. Ethmoid region in ventral view of *Pimelodus grosskopfi*, DU-F-919, B. Right mandible of *Exallodontus aguanai*, DU-F-977, Single scale bar for both = 2 mm.

1979, field number T-13-79. DU-F-1028, 1, 90 mm, near Puerto Ordaz, N of Isla Fajardo, 180 n mi from sea buoy, 8°24′N, 62°40′W, 23 Nov 1979, field number T-84-79. Territorio Federal Delta Amacuro (all collected by R/V *Eastward* in Río Orinoco). DU-F-1029, 1, 136 mm, near Barrancas, 139 n mi from sea buoy, 8°44′N, 62°07′W, 17 Feb 1978, field number JGL-19-78. DU-F-1030, 4, 159-180 mm, S of Isla Portuguesa, 117 n mi from sea buoy, 8°36′N, 61°48′W, 20 Feb 1978, field number JGL-44-78. DU-F-1031, 1, 86 mm, near Los Castillos, 161 n mi from sea buoy, 8°31′N, 62°24′W, 10 Nov 1979, field number T-20-79. DU-F-1032, 1, 95 mm, near Los Castillos, 160 n mi from sea buoy, 8°32′N, 62°23′W, 10 Nov 1979, field number T-27-79. DU-F-1033, 1, 107 mm, downstream from Isla Portuguesa, 116 n mi from sea buoy, 8°36′N, 61°47′W, 14 Nov 1979, field number T-60-79.

Diagnosis.—The same as that of the genus.

Description.—Lateral, dorsal and ventral views in Figs. 7 and 8 illustrate head and body shape, form and position of fins, and pigment pattern. Variational data for morphometric and meristic characters are given in Tables 1–3. Additional features are described and compared in the section on phylogenetic relationships.

Cranial roof partly visible through thin and transparent integument; bones near midline coarsely sculptured with anastomosing, longitudinally-trending ridges; sphenotic and temporal region bones sculptured with irregularly oriented ridges (cranial bone texture not to be confused with overlying dendritic sensory canal branches, see below). Anterior cranial fontanelle open from level of posterior nares to posterior margin of orbit, followed posteriorly by a shallow groove to level of pterotic; fontanelle and groove covered above with pale integument. Posterior cranial fontanelle a small or minute foramen at base of supraoccipital process (Fig. 6A).

Mouth distinctly subterminal; snout projecting beyond upper lip by a distance about equal to horizontal diameter of eye. Mouth opening anteroventrally; margin of closed mouth smoothly curved; one or two rows of premaxillary teeth exposed; corner of closed mouth a little anterior to a vertical from anterior edge of posterior naris; gape width about equal to distance across lower margins of orbital rims. Upper lip smooth or with a few coarse papillae immediately adjacent to premaxillary teeth; the lower lip weakly plicate; both lips without accessory folds paralleling tooth rows. Fleshy rictal fold in a pocket behind corner of mouth, scarcely protruding above general surface of head; a shallow groove extends anterodorsally from rictal fold to terminate anterior to base of maxillary barbel; ventral to rictal

Table 1.—Standard lengths and proportionate characters for *Exallodontus aguanai* expressed in thousandths of the standard dimensions given in parentheses (SL—standard legnth, CPL—caudal peduncle length, ADL—adipose fin length, AFB—anal fin base, HL—head length); means for Orinoco sample followed by ranges in brackets, and sample size.

Measurement	Orinoco sample	Holotype MBUCV 18930	Amazon sample		
			ANSP 150177	ANSP 150178	INPA 4550
Standard length (mm)	115.4 [43.5–207.0] 52	207.0	91.9	59.5	140.0
Predorsal fin length (SL)	310 [283–342] 52	292	331	304	296
Prepectoral fin length (SL)	203 [174–257] 32	179	220	190	204
Preanal fin length (SL)	643 [615–671] 32	651	659	640	640
Head length (SL)	225 [191–253] 52	204	247	220	214
Caudal peduncle length (SL)	257 [227–279] 52	265	252	245	261
Caudal peduncle depth (CPL)	292 [263–338] 32	290	293	284	287
Adipose fin length (SL)	463 [402–498] 52	479	469	431	472
Adipose fin height (ADL)	137 [104–206] 32	113	163	116	144
Anal fin base (SL)	92 [76–104] 20	85	96	—	109
Anal fin height (AFB)	2058 [1798–2387] 20	2080	2000	—	1907
Pelvic fin length (SL)	210 [183–243] 52	195	219	208	212
Urogenitial papilla-anal fin (SL)	190 [132–238] 38	190	180	142	209
Pectoral spine length (SL)	157 [139–180] 48	158	158	153	170
Dorsal spine length (SL)	140 [116–178] 48	116	140	122	138
Dorsal fin base (SL)	143 [134–160] 18	137	133	131	140
Dorsal fin height (SL)	170 [146–190] 31	161	163	163	186
Body depth (SL)	202 [171–242] 52	215	197	182	211
Body width (SL)	173 [155–190] 52	170	165	184	169
Posterior cleithral process (SL)	88 [77–97] 32	85	92	88	79
Bony interorbital (HL)	258 [229–286] 32	258	293	267	264
Interocular (HL)	319 [294–350] 37	334	333	307	301
Eye diameter (HL)	108 [83–135] 51	100	128	102	90
Snout length (HL)	466 [433–514] 52	488	465	456	458
Internarial length (HL)	217 [181–246] 38	199	213	211	194
Internarial width (HL)	183 [172–194] 18	180	183	183	167

fold a thin submandibular groove extends about ½ distance to symphysis. Jaw teeth (Fig. 2) described in diagnosis of genus; no teeth on palate. Upper oral valve broader and longer than premaxillary tooth bands; with a small, raised epithelial patch on the midline (scanning electron micrcoscope observations made on similar median structures in several other catfishes reveal the presence of many taste buds).

Barbels thin, proximally flattened but lacking membranous edges. Maxillary barbel reaching to beyond origin of anal fin; inserted midway between anterior nostril and posterior end of rictal fold. Mental barbels inserted in advance of gular fold apex, in a curved line parallel to lower jaw margin. Inner mental barbels 1.5–2 times closer to gular fold than to margin of lower jaw; inner mental barbels reach to about 0.5 length of depressed pectoral fin. Outer mental barbels reach to 0.5 length or more of depressed pelvic fin. Gular fold overlying a deep groove, its sides meeting in an obtuse angle; each side equal to or a little greater than distance between inner and outer mental barbels. Gill membranes free, diverging at once from gular fold apex, supported by 8 branchiostegal rays (1 on posterior ceratohyal + 1 on cartilage between ceratohyals + 6 on anterior ceratohyal). Gill rakers on first branchial arch 19–21 (5–6 on upper limb, 1 at angle, 13–14 on lower limb, n = 4). Upper and lower pharyngeal teeth robust

Table 2.—Frequency distribution of anal-fin ray counts in *Exallodontus aguanai.*

Total rays	11	12			13			14
Formulae	iv7	v7	iv8	vi7	v8	iv9	v9	iv10
Venezuela (n = 19)	4	1	6	1	3	2	1	
Amazon (n = 5)						1	2	2

with straight to scarcely recurved crowns. Anterior nostril located dorsally on snout, behind snout tip by about its own diameter and a little anterior to a line between anterior edges of maxillary barbel bases; its rim tubular and flaring; its aperture about 0.3 of orbital diameter. Posterior nostril medially offset from a line between anterior border of orbit and anterior nostril; its rim a thin membrane elevated anteriorly and curving ⅔ distance around aperture, incomplete posteriorly; its aperture ovoid with transverse principal axis. Eye small, centered on midlength of head and about 45° above mid-frontal plane. Orbital rim fleshy and free. Orbital opening ovoid, its vertical diameter contained 1.3–2 times in horizontal diameter; visible part of eye comprising mostly pupil and lens.

Head lateralis system with superficial, many-branched tubes that lead to minute pores on nape, top of head, cheeks, operculum and mandible. (The complex dendritic structure of the lateralis system precludes external enumeration and comparison of the primary branches that exit through dermal bone foramina. This subject is under study as part of a broader investigation of pimelodid systematics.) Lateral line canal complete, reaching onto base of middle caudal rays, curved slightly ventrad over hypurals; its anterior tubes dendritic over lateral cutaneous area; tubular ossicles surround lateral line to below dorsal-fin base, these not visible externally.

Dorsal fin with eight rays: a spinelet, a strong and pungent spine, and 6 soft rays; bases of last two rays separate; distal margin gently convex; length of last ray a little less than half that of first. Spinelet (ray 1) with a narrow median crest recalling crest on supraoccipital process. Dorsal spine with a compressed, anterior median ridge, sharply elevated proximally where it is ligamentously tied to spinelet. Dorsal spine (ray 2) with a few small retrorse dentations posterodistally. Adipose fin long, high, straight-margined for most of its length, ending in a short free lobe; its origin close to dorsal fin; its highest point anterior to anal-fin origin. Caudal fin deeply forked, its lobes with concave inner margins; upper lobe produced, its outer principal ray filamentous; shortest middle caudal rays contained in longest upper rays 4–5 times, and about 3 times in longest lower rays; principal caudal rays 1,7–8,1; procurrent caudal rays 12–15 upper, 10–18 lower. Anal fin (Fig. 6B) with a concave distal margin; anal-fin rays 11–14, the first 4–6 rays simple (Table 2), anterior 3 branched rays and longest simple ray produced to form a blunt paddle-like

Table 3.—Frequency distribution of vertebral counts in *Exallodontus aguanai.* Precaudal vs. caudal distinction indeterminate in one dry skeleton from Venezuela.

	Precaudal			Caudal					Total		
Classes	16	17	18	29	30	31	32	33	46	47	50
Venezuela (n = 5)	3	1		1	1	2			2	3	
Amazon (n = 2)		1	1				1	1			2

projection in largest specimens (of six dissected all are female); fin rays of paddle exceeding tip of last anal ray but not reaching below end of adipose fin.

Pectoral fin with a spine plus 10–11 soft branched rays; its distal margin truncate except first soft ray a little longer than spine tip; depressed pectoral fin reaches to below fourth–fifth dorsal-fin soft rays and short of a vertical at pelvic-fin origin. Pectoral spine (Fig. 9) strong, sharp; no or weak anterior distal serrae, but with antrorse to erect anterior dentations along proximal ¾, and retrorse dentations present along most of posterior margin. Anterior dentations very strongly developed in small specimens, becoming progressively less prominent and more crowded basally. Posterior dentations unicuspid and mostly regularly spaced. Posterior cleithral process deep and acutely triangular with a sharply pointed tip; its surface ornamented with fine osseous ridges and a few weakly developed tubercles. No axillary-pore below postcleithral process. Pelvic fin with 6 soft rays, the first simple. Pelvic-fin origin below penultimate dorsal-fin ray; its distal margin truncate, except first branched ray a little longer than first, pelvic-fin length contained in SL 4.1–5.5 times; distance between tip of depressed pelvic fin and anal-fin origin about equal to anal-fin base length.

Total vertebrae 46–50, 16–18 precaudals and 29–33 caudals (Table 3).

Urogenital papilla with no apparent sexual dimorphism; located in a shallow depression immediately behind anus and between pelvic fins about midway along length of their inner fin rays.

Color in alcohol.—Most specimens preserved in alcohol are countershaded with an abrupt demarcation at lateral line. Dorsal to the lateral line, sides and fleshy part of nape are dark to light grayish-purple or grayish-tan; cheeks and sides of snout similarly colored. Sides ventral to lateral line, venter of body, head and snout tip much lighter, often white. Dorsum of head dull yellow (imparted by underlying bones) and finely streaked with irregular lines of dark chromatophores. Narial region flanked medially by short dark stripe dorsal to nasal bone, and usually by a short dark stripe dorsal to "lacrimal." Barbels dusky dorsally, white ventrally. Fins hyaline distally, but interradial membranes pale white to yellowish proximally. Some specimens have dark lines on anterior margins of dorsal-fin rays. In most specimens each caudal-fin lobe has a dark medial stripe tapering caudad from an obscure basal blotch over middle 3 or 4 rays.

Color upon capture.—Specimens from both the Orinoco and Amazon have a metallic green to brassy sheen on nape to either side of supraoccipital process, sides dorsal to pectoral fin, sides and venter of head. Dorsum of head over skull bones dark gray to black. Flanks, venter, adipose fin base, barbels, pectoral and dorsal spines white. All fins dull yellow-orange, and each caudal-fin lobe has a longitudinal dark gray to black stripe over middle 3 or 4 rays.

Distribution and ecology.—*Exallodontus* presently is known to occur in Venezuela in the mainstem of the lower Río Orinoco and in middle Orinoco basin in the Apure and Meta rivers, and in the Amazon mainstem near Iquitos, Peru and Manaus, Brazil (Fig. 10). All specimens have been taken by bottom trawls in the main channels of large rivers at depths ranging from about 3–35 m, in current speeds exceeding 1.5 m/sec, and on sandy to detritus-covered substrates. We expect that further collecting with trawls in large rivers of the Amazon and Orinoco systems will reveal a wider distribution of this species. *Exallodontus aguanai* is commonly associated with other catfishes (pimelodids, doradids, cetopsids, loricariids), electric fishes (sternopygids, apteronotids, rhamphichthyids, hypopomids) and freshwater sciaenids (López et al. 1985).

Variation.—Despite the large distance between the Orinoco and Amazon samples of *E. aguanai,* there is no apparent differ-

entiation. The two Peruvian specimens have 50 vertebrae in contrast to 46–47 in the Orinoco subsample (Table 3). However, a total intraspecific range of variation of five vertebrae is not unexpectedly high for catfishes.

Etymology.—The specific name, *aguanai*, honors Sr. Leonidas Aguana of the Instituto de Zoología Tropical, Universidad Central de Venezuela, whose long friendship with the authors and intrepid collaboration in the field have contributed greatly to this research and to Venezuelan ichthyology.

Relationships.—This section begins with a delimitation and phylogenetic diagnosis of the subfamily Pimelodinae to which *Exallodontus* belongs. We then review a nested set of synapomorphies, in descending hierarchical order, that relate *Exallodontus* to subgroups of pimelodines. Inference of character polarities is based on the outgroup framework outlined above in Methods, and the outgroup taxa and specimens are listed below under comparative materials. Although we are unable to completely resolve the sister group relationship of *Exallodontus*, we have discovered sufficient evidence to develop a hypothesis on its proximate relatives. The results of this phylogenetic analysis are summarized in Fig. 1. Except for the subfamily Pimelodinae, we use informal names to refer to various generic groups. We believe that formal naming and diagnosing of these subgroups would be premature in light of ongoing research and manuscripts in preparation by us and Donald J. Stewart.

Subfamily Pimelodinae

Membership.—Based on examination of available specimens (those represented by skeletal specimens marked by *) or literature descriptions, we assign the following nominal genera to the Pimelodinae (see also Fig. 1): *Aguarunichthys, Bagropsis, Bergiaria, Brachyplatystoma**, *Calophysus**, *Cheirocerus**, *Conorhynchos, Duopalatinus**, *Exallodontus**, *Goslinia**, *Hemisorubim**, *Hypophthalmus**, *Iheringichthys**, *Leiarius**, *Luciopimelodus, Megalonema**, *Merodontodus, Perrunichthys, Parapimelodus**, *Paulicea**, *Phractocephalus**, *Pimelodina**, *Pimelodus**, *Pinirampus**, *Piramutana, Platynematichthys**, *Platysilurus**, *Platystomatichthys**, *Pseudoplatystoma**, *Sorubim**, *Sorubimichthys**, *and Steindachneridion**.

Diagnosis.—Three synapomorphic characters support the group of nominal genera here united as the Pimelodinae. For additional description and illustrations of these characteristics see Lundberg & McDade (1986), Lundberg et al. (1988), and Lundberg et al. (1991).

(1) Dendritic arrangement of lateral line tubes in skin of snout, cheek and nape (Fig. 11A). Other pimelodids and most other catfishes, including diplomystids, have simple unbranched lateralis tubes.

(2) Uniquely shaped, much elongated articulation surface on lateral ethmoid for palatine (Fig. 11B). Plesiomorphically this joint surface has the form of a foreshortened, inverted triangle as is found in other pimelodids and other outgroup catfishes, including diplomystids and †*Hypsidoris*.

(3) Deep sutural joint between fifth and sixth centra (Fig. 12A & B). In other pimelodids and most other catfishes, including diplomystids and †*Hypsidoris*, there is a typical intervertebral joint between the fifth and sixth centra. *Megalonema*, which we place in the Pimelodinae, is exceptional in having a normal, non-sutural joint between vertebrae five and six (Stewart 1986a). Howes 1983:37, reported for *Megalonema* "the 5th and 6th centra fused within the vertebral complex," based on a dissected specimen; our observations concur with Stewart's and are made on cleared and stained specimens. We interpret this as a reversal in *Megalonema*, not a primitive characteristic, because *Megalonema* possess the nested synapomorphies for three subgroups within the subfamily as outlined

below: "Group A," the "*Calophysus-Pimelodus clade,*" and, in part, the "*Calophysus* group."

Lundberg et al. (1988) listed another putative synapomorphy for the clade here referred to as Pimelodinae: a bony canal, for an asymmetrically enlarged postcardinal vein, on the ventral surface, left side, of the Weberian complex at the angle between the centra and transverse processes. We have since observed that this feature occurs more broadly among pimelodids and in some other catfish families (e.g., Siluridae, Bornbusch 1988). Among pimelodids the asymmetry of veins and left side bony canal are present in *Pseudopimelodus apurensis* and *Zungaro zungaro.* Based on other evidence, these two species belong to the monophyletic subfamily Pseudopimelodinae that also includes the nominal genera *Lophiosilurus* and *Microglanis* (Lundberg et al. 1988, Lundberg et al. 1991). Available representatives of the last two genera lack the venous and skeletal asymmetry. All other pimelodids examined, in particular the Rhamdiinae (Lundberg et al. 1991, = Group B of Lundberg et al. 1988), have symmetrical postcardinal veins and lack bony canals. Consequently, the derived asymmetrical condition of the postcardinal veins is incongruent with current hypotheses of relationships. It remains to be determined if the asymmetrical structures are relevant to more inclusive taxonomic levels than suggested by Lundberg et al. (1988).

Subfamily name.—The Pimelodinae takes its name from *Pimelodus* Lacépède (1803), the oldest-named member genus. Günther (1864) employed the name Pimelodina (not the genus) for an assemblage nearly equivalent to the Pimelodidae of modern authors. The subfamily name Pimelodinae has been applied to more or less the same group. Eigenmann & Eigenmann (1890) first used Pimelodinae for a subfamily within the Siluridae, then an ample family that included most catfishes (Bleeker 1862, Günther 1864, Gill 1872). Eigenmann & Eigenmann's Pimelodinae excluded *Calophysus,* which they placed in its own subfamily, and included genera that are now placed in other subfamilies (Rhamdiinae and Pseudopimelodinae). With the acceptance of Regan's (1911) catfish families, the Pimelodinae became a subfamily within the Pimelodidae. While various relatively apomorphic pimelodid genera were set off in their own subfamilies, the Pimelodinae has remained a large, poorly defined and catch-all group. Thus, Driver (1919) established the Luciopimelodinae for *Luciopimelodus* and *Megalonema* (Driver also included *Perugia* which has been shown to be a synonym of *Pinirampus* by Stewart 1986a). Schultz (1944) united in the Sorubiminae the nominal genera *Brachyplatystoma, Duopalatinus, Hemisorubim, Leiarius, Perrunichthys, Paulicea, Phractocephalus, Platynematichthys, Platysilurus, Platystomatichthys, Pseudoplatystoma, Sorubim, Sorubimichthys,* and *Steindachneridion.* Also, apparently based on shared absence of certain obvious specializations, the auchenipterid catfishes were included in the Pimelodinae by Eigenmann & Allen (1942), but their classification position has never been followed.

"*Group A.*"—Within the taxon here named Pimelodinae, Lundberg et al. (1988) proposed an informally-named "Group A" that is the sister group to a small clade comprising *Phractocephalus, Leiarius* and *Perrunichthys* (Fig. 1). *Exallodontus* belongs to "Group A."

In support of "Group A" Lundberg et al. (1988), following the lead of Howes (1983), listed one synapomorphic feature: osseous "aortic tunnel" or canal on ventral side of Weberian centra (Fig. 12B ao. ca.). The aortic canal, containing the dorsal aorta, is formed by extension of the superficial ossification over the midventral aortic groove usually from centrum 1 to 5 or 6 (but restricted to the compound Weberian centrum in *Megalonema*). Other pimelodids and most other catfishes, including diplomystids and †hypsidorids, have an open

midventral aortic groove on these centra (Fig. 12A ao. gr.). A more extensive type of aortic tunnel running from the basioccipital to beyond the sixth vertebra is found in the Ariidae, and small bridges of bone span the aortic groove in some doradids and *Ageneiosus.*

Calophysus-Pimelodus clade.—Four putative synapomorphies lead to a hypothesis of monophyly of a large group of genera within "Group A" comprising the "*Calophysus* group" (Stewart 1986a), *Megalonema,* and our "*Pimelodus* group" (see below and Fig. 1). Stewart (1986a) presented evidence for monophyly of a "*Calophysus* group" including the genera *Calophysus, Pinirampus, Pimelodina, Luciopimelodus* and *Aguarunichthys.* Stewart excluded *Megalonema* from the "*Calophysus* group," but noted that these taxa share derived characteristics of the slender pectoral spine, high pectoral fin-ray count, and loss of the posterior cleithral process. We tentatively place *Megalonema* as the sister taxon to the "*Calophysus* group." Howes (1983) suggested that *Hypophthalmus,* usually isolated in its own family, may be closely related to a group of pimelodids including some members of our "*Calophysus-Pimelodus* clade." In agreement with Howes, we classify *Hypophthalmus* among the Pimelodidae (and Pimelodinae). However, *Hypophthalmus* does not share the synapomorphies that support the "*Calophysus-Pimelodus* clade" and we consider its position to be indeterminate within the subfamily. *Exallodontus* is a member of the "*Calophysus-Pimelodus* clade." The four synapomorphies of this lineage follow.

(1) Ossified posterior part of ethmoid plate, i.e., posteroventral part of mesethmoid, has parallel sides, and abruptly-rounded, to nearly right-angled, corners (Fig. 13A; see also fig. 5B of *Pimelodus pictus,* Lundberg & McDade 1986; and fig. 1c of *Pimelodina flavipinnis,* Stewart 1986a). Also, because the vomer lacks prominent lateral processes, the synchondral (sometimes sutural) joint between the mesethmoid and lateral ethmoid is widely exposed. In its plesiomorphic form, found in pseudopimelodines (Lundberg et al. 1991), other pimelodines, and most other catfishes including diplomystids and †hypsidorids, the ethmoid plate has concave sides and acutely-angled posterolateral corners. Lundberg & McDade (1986), Ferraris (1988) and Lundberg et al. (1991) described another uniquely and separately derived form of the lateral synchondral joint between the mesethmoid and lateral ethmoid that characterizes the subfamily Rhamdiinae.

(2) Mesethmoid cornua abruptly deflected ventrad and with a small or no median cleft (Fig. 13A; see also Lundberg & McDade 1985: fig. 5B, Stewart & Pavlik 1985: fig. 2; Stewart 1986a: fig. 1c). In other pimelodids and catfishes that have mesethmoid cornua, including diplomystids and †hypsidorids, these structures taper anterolaterally in the horizontal plane without a marked downward deflection.

(3) Coronoid process of mandible very deep, and formed of steep, slender processes of dentary and angular part of anguloarticular bones (Fig. 13B). The coronoid process is relatively much less prominent in other pimelodids and most other catfishes, including diplomystids and †hypsidorids (e.g., Lundberg & McDade 1986: fig, 9).

(4) "Cleithral ring" comprised of supracleithrum's lateral and medial processes plus fourth transverse process that together surround dorsal limb of cleithrum (Fig. 12B cl. ring). Despite debate over the composition of the upper element of the catfish shoulder girdle, Lundberg (1975) and Fink & Fink (1981) would agree that the ventral part of the bone that articulates with the cleithrum should be termed supracleithrum. In most pimelodids, and catfishes generally, including diplomystids and †hypsidorids, the ventral part of the supracleithrum has a deep "cleithral notch" flanked by two parallel or

divergent processes that together clasp the pointed dorsal limb of the cleithrum (Fig. 12A cl. notch; see also Lundberg 1975: fig. 2B and C). Primitively, the two processes of the supracleithrum are unequally developed: the lateral process is the longer, whereas the medial process is shorter and has a major articulation site on its posterior surface for the expanded anterior limb of the transverse process of vertebra four. In the formation of the "cleithral ring" of the "*Calophysus-Pimelodus* clade," the fourth transverse process is drawn out posteriorly and converges on the medial surface of the supracleithrum's lateral process with which it has a firm, ligamentous union. Also, the supracleithrum's lateral process is drawn out posteroventrally to make contact with a flange of the cleithrum that projects dorsal to the otherwise concave posterior margin between the upper cleithral limb and posterior cleithral process.

"*Pimelodus group.*"—Within the "*Calophysus-Pimelodus* clade" we have identified one putative synapomorphy for a monophyletic group including the nominal genera *Cheirocerus, Duopalatinus, Exallodontus, Iheringichthys, Parapimelodus, Pimelodus, Platysilurus,* and *Platystomatichthys.* The genera *Bagropsis, Bergiaria,* and *Conorhynchos* are tentatively included in this lineage based on external characters, but we have not examined skeletonized specimens. The synapomorphy supporting this clade is: tranverse processes of vertebrae four and five are sutured to their lateral edges (Fig. 12B). This broad union of the transverse processes creates a longer and broader osseous sheet over the swmbladder than in any other pimelodids and most other catfishes, including diplomystids and †hypsidorids. Lundberg & McDade (1986) and Lundberg et al. (1991) described and illustrated various conditions of the form of the fourth, fifth and sixth transverse processes in the Pimelodidae. The primitive condition in the family, as identified by outgroup comparison, is found in *Leiarius, Microglanis* (Lundberg & McDade 1986: fig. 4E), *Pseudopimelodus, Lophiosilurus* and *Zungaro* in all of which the posterior limb of the fourth transverse process tapers to a blunt tip, and there is a deep notch between this process and the much smaller fifth transverse process. In other pimelodid genera a distinct and usually deep notch between the fourth and fifth transverse processes is retained (Fig. 12A).

Within the "*Pimelodus group*" the relationships of *Bagropsis, Bergiaria,* and *Conorhynchos* have not been studied by us and are unresolved. The other genera of the group can be assigned to two smaller clades. The first clade includes *Platysilurus* and *Platystomatichthys* whose close relationship is indicated by two features that may be unique among catfishes: (1) narrow dorsomedian groove extending from posterior fontanelle across supraoccipital process onto anterior nuchal plate (supraneural), and (2) greatly hypertrophied maxillary bone that reaches, within its barbel, to about the anal-fin origin. The second clade within the "*Pimelodus group*" contains *Cheirocerus, Duopalatinus, Exallodontus, Iheringichthys, Parapimelodus,* and *Pimelodus.* This alignment is suggested by the apomorphically extensive posterior development of superficial ossification of the Weberian complex centra that ventrally covers the seventh centrum (Fig. 12B). Other pimelodids (except one known to us) and most other siluriforms, including diplomystids and †hypsidorids, have the seventh centrum exposed ventrally and the superficial ossification restricted to more anterior vertebrae (Fig. 12A). The single exception among the pimelodids is *Brachyplatystoma rousseauxi* that has the seventh centrum completely covered by superficial ossification. We have interpreted this as a homoplasious similarity between *B. rousseauxi* and the "*Pimelodus* group." *B. rousseauxi* not only lacks the other synapomorphies of the "*Calophy-*

sus-Pimelodus clade" and the *Pimelodus* group, but instead shares several unique apomorphies with species currently classified in the nominal genera *Brachyplatystoma* and *Goslinia* (Nass, in prep.).

Pimelodus.—In the literature dating back to at least Eigenmann & Eigenmann (1888, 1890), *Exallodontus aguanai* would be identified as a species of *Pimelodus*. For the reasons given above we have chosen to describe *Exallodontus* as a new genus. Assignment of *E. aguanai* to *Pimelodus* would make a bad situation worse. *Pimelodus* has an old and complex taxonomic history involving catfishes from all over the world. Even restricted as it is now to a group of South American catfishes, *Pimelodus* is complex (e.g., *P. heteropleura* is a member of the Rhamdiinae, closely similar to *Brachyrhamdia* and *Pimelodella*), the species-level taxonomy of the species and populations similar to the type species *P. maculatus* is unsettled, and the genus has not been diagnosed in an explicit phylogenetic framework. A revision of *Pimelodus* is underway by D. J. Stewart.

Here we offer some data on a character complex that might prove useful in a phylogenetic diagnosis of *Pimelodus*. Most catfishes have a relatively simple pattern of trigeminofacial nerve foramina in the prootic and pterosphenoid in contrast to other otophysans and teleosts (Howes 1983). Our survey suggests that the majority of siluriform families have one large foramen on the prootic-pterosphenoid boundary (Fig. 14A), or rarely in the prootic alone, for the major branches of the fifth and seventh cranial nerves, i.e., the maxillary and mandibular branches of the trigeminal, and the hyomandibular and palatine trunks of the facial. Separate small foramina are usually present for the superficial ophthalmic branches of the fifth and seventh nerves. Diplomystids (also, Howes 1983, lists some other catfishes) have the single trigeminofacial foramen confluent with the optic foramen in the orbitosphenoid. The single trigeminofacial foramen is also the general condition for pimelodids, being found in the subfamilies Rhamdiinae and Pseudopimelodinae, and most Pimelodinae. In a few Pimelodinae, including *Calophysus* (Fig. 14B), *Goslinia*, *Hypophthalmus* (Howes 1983: fig. 17), *Pimelodina*, and *Sorubim*, the main branches of trigeminal and facial exit through their own separate foramina. Outside of the Pimelodidae the facial nerve foramen is subdivided in some silurids (*Belodontichthys*, *Kryptopterus*, *Silurus*). In several species of *Pimelodus* (*blochi*, *grosskopfi*, *coprophagus*, cf. *clarias* from the Río Magdalena, and *pictus*, but not *ornatus* or *altissimus*) there is an additional foramen (Fig. 14C). In these species there are three separate foramina, one each for the maxillary, mandibular and hyomandibular (facial) nerves. These species also have smaller foramina and canals through the prootic and pterosphenoid. Details of this complex anatomy remain to worked out across a wide swath of pimelodids. At present it is clear, however, that many species of *Pimelodus* share an unusual derived condition of the trigeminofacial foramina. That *Exallodontus* lacks this feature and is like the majority of other pimelodids is consistent with our description of the genus as taxically distinct from *Pimelodus*.

Comments on some papers by Howes.—As noted above, Howes (1983) argued for a relationship of *Hypophthalmus* within the Pimelodidae. We agree and assign this highly specialized genus to the Pimelodinae. Howes (1983) also proposed "three major groups" of pimelodids and listed exemplar members and some characters for each. Howes' third group (*Rhamdia*, *Pimelodella*, *Heptapterus*) includes members of the Rhamdiinae (Lundberg & McDade 1986, Lundberg et al. 1991). The characters listed by Howes for this group are relatively plesiomorphic among pimelodids, i.e., unencapsulated swimbladder without cecae or compressor muscles, and five vertebrae included in the Weberian complex. Howes'

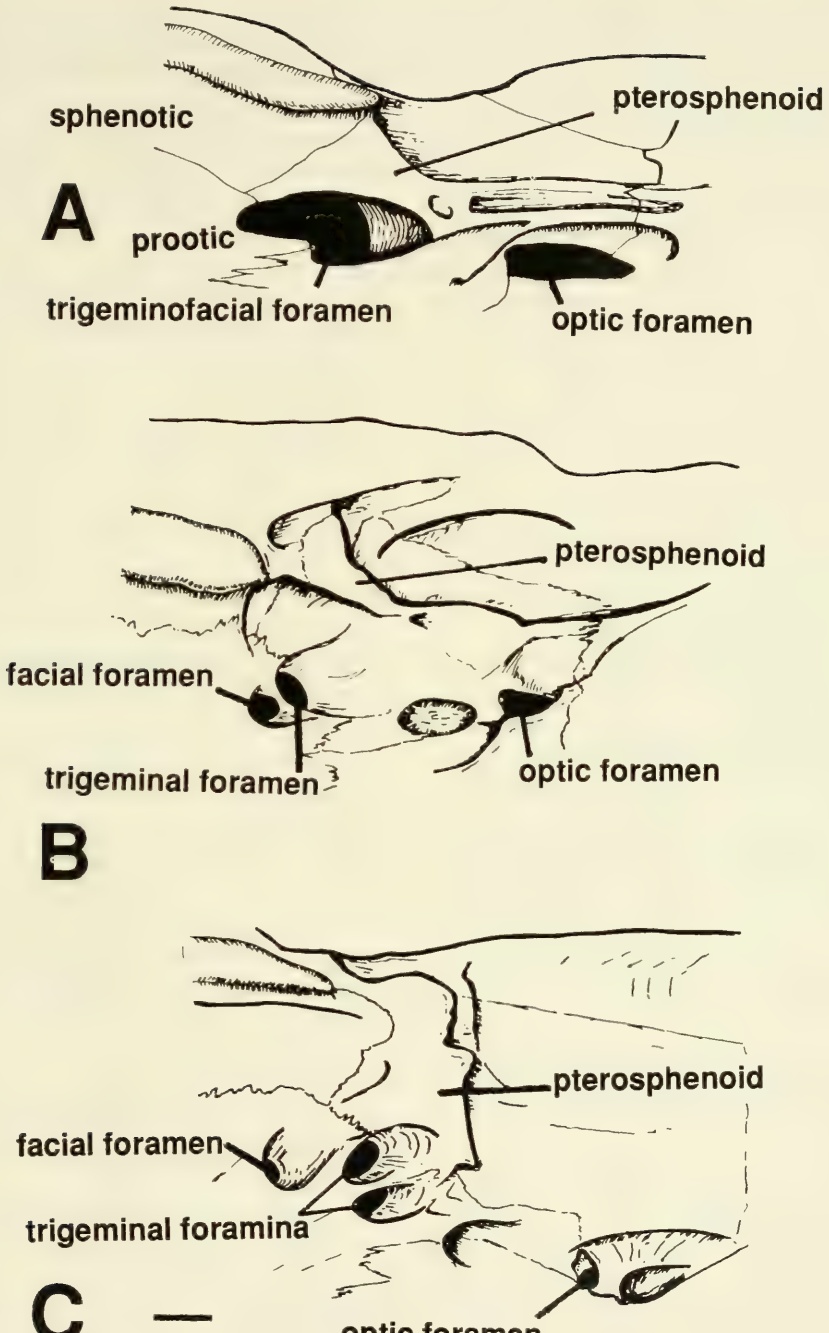


Fig. 14. Trigeminofacial foramina in A. *Rhamdia wagneri,* DU-F-1021, B. *Calophysus macropterus,* DU-F-985, C. *Pimelodus grosskopfi,* DU-F-919, Scale bar for A and C = 2 mm, for B = 1 mm.

first group (*Calophysus, Iheringichthys, Luciopimelodus, Megalonema, Parapimelodus, Pimelodina, Pinirampus, Pimelodus* (part)) plus his second (*Pseudoplatystoma, Hemisorubim, Sorubim, Pimelodus* (part)) include members of our "Group A" diagnosed, as above, by the aortic tunnel. The characters listed by Howes for his second group are also relatively plesiomorphic or uncertainly apomorphic among catfishes, i.e., unencapsulated swimbladder with muscular walls, and a maxillary barbel retractor muscle. Howes characterized his first group as having partially encapsulated swimbladder, but this is contradicted by our specimens of *Iheringichthys* and *Parapimelodus,* and we have not observed specimens of *Pimelodus* with such a condition. Otherwise this group corresponds with Stewart's "*Calophysus* group."

Howes (1983) also noted the presence of two oddly-shaped pterygoid bones anterior to the metapterygoid in some members of his first group: *Calophysus, Iheringichthys, Parapimelodus, Pinirampus,* and *Pimelodus maculatus.* These bones are a "scythe-shaped" medial element between the lateral ethmoid and palatine, and a slender rod-like element lateral to the palatine. Respectively, we would term these bones, following Regan (1911), entopterygoid (=mesopterygoid or endopterygoid) and ectopterygoid. We also find similarly shaped entopterygoid and ectopterygoid elements in *Cheirocerus, Duopalatinus, Exallodontus, Megalonema, Pimelodina,* and *Pimelodus* (all species examined). These genera plus the ones cited by Howes are members of the "*Calophysus-Pimelodus* clade," but this group is not strictly characterized by such pterygoid bones. *Platysilurus* and *Platystomatichthys,* members of the clade, have instead plate-like anterior pterygoid elements, and *Leiarius,* not a member of the clade, has the scythe-shaped and rod-like configuration. Various other conditions of the anterior pterygoid bones and associated tooth plates in the Pimelodinae remain to be described and their distributions determined precisely. At present we do not employ the form of the pterygoid bones in diagnoses of pimelodine subgroups.

The terminology of the pterygoid elements has been problematical. In a recent paper on the homologies of catfish pterygoids Howes & Teugels (1989) concluded that the two anterior elements are fragmented parts of the entopterygoid or sesamoid bones formed in ligaments. Howes & Teugels (1989) consider the ectopterygoid and entopterygoid to be represented in catfishes by ventral and anterodorsal osseous laminae fused with the metapterygoid. Given current information this appears to be an unnecessarily complicated interpretation. From Howes & Teugels' (1989) developmental series of *Corydoras* (Callichthyidae), *Clarias* (Clariidae) and *Ageneiosus* (Ageneiosidae), and ours of *Pinirampus* (Pimelodidae), entopterygoid and ectopterygoid centers of ossification are not seen to form separately and then to fuse with the metapterygoid. Rather, as Howes & Teugels (1989) correctly describe, the metapterygoid begins as an endochondral bone on the pterygoquadrate cartilage and later anterodorsal and ventral laminae extend outward from it. This does not appear to be different from the endochondral quadrate and hyomandibula which in many catfishes develop membranous, laminar extensions into surrounding connective tissues. The most primitive form of the anterior pterygoids in siluriforms appears to be that of diplomystids, and here we disfavor Arratia's (1987) terminology for these as "additional pterygoid" and "bone 4 of McMurrich." In diplomystids there are two small toothless plates anterior to the metapterygoid, the more lateral of which is at the posterior tip of the palatine, in line with the main axis of the metapterygoid, and the other is offset medially. Although these bones are not in sutural contact they have the expected relative positions of ectopterygoid (more lateral and contacting the palatine) and entop-

terygoid (more medial). It is our belief that the most parsimonious interpretation of the scythe-shaped and rod-like elements of some pimelodids is that they are apomorphic conditions of the entopterygoid and ectopterygoid respectively but that their level of taxonomic generality within the subfamily Pimelodinae remains to be determined.

Comparative material examined.—Listed below are first, alcohol preserved specimens of pimelodines used in morphometric comparisons of *Exallodontus,* and, second, skeletal specimens by subfamilies of Pimelodidae and, lastly, other families.

Alcohol preserved specimens.—Number of specimens and range of standard lengths follow catalogue number. *Calophysus macropterus* DU-F-(JGL 30-78), 2, 168–175, Venezuela, Orinoco Delta region; DU-F-(JGL 19-78), 2, 141–155, Venezuela, Orinoco Delta region; *Duopalatinus emarginatus* USNM 44974, 1, 176, Brazil, Rio das Velhas; *Duopalatinus peruanus* ANSP 158185, 1, 139, Venezuela, Puerto Ayacucho; ANSP 160189, 3, 80–86, Venezuela, Amazonas; ANSP 160203, 1, 80, Venezuela, Amazonas; MBUCV-V-14991, 2, 113, Venezuela, Río Arauca; *Pimelodina flavipinnis* DU-F-(T 77-79), 1, 141, Venezuela, Orinoco Delta region; DU-F-(HLR 40-79), 4, 129–232, Venezuela, Orinoco Delta region; DU-F-(HLR 22-79), 2, 85–123, Venezuela, Orinoco Delta region; "*Pimelodus* A" from the Orinoco, DU-F-(HLR 6-79), 4, 132–170, Venezuela, Orinoco Delta region; DU-F-(HLR 12-79), 2, 118–152, Venezuela, Orinoco Delta region; DU-F-(HLR 13-79), 1, 156, Venezuela, Orinoco Delta region; DU-F-(HLR 19-79), 1, 98, Venezuela, Orinoco Delta region; DU-F-(HLR 22-79), 1, 167, Venezuela, Orinoco Delta region; DU-F-(JGL 40-78), 3, 46–122, Venezuela, Orinoco Delta region; "*Pimelodus* cf. A" from the Amazon, FMNH 41508, 2, 121–135, Brazil, Pará; USNM 121857, 3, 115–145, Brazil, Belém; FMNH 52572, 1, 177, Brazil, Amazonas; IU 4266 (at CAS), 2, Peru, Pebas; CAS 6612, 1, Brazil, Belém; CAS 6649, 2, Brazil, Belém; CAS 6650, 1, Brazil, Belém; CAS 6582, 1, Brazil, Belém; SU 22178 (at CAS), 22, Brazil, Pará; *Pimelodus altissimus* CAS 55369, Paratype, 1, 166, Peru, Río Ucayali; *Pimelodus altissimus* (a complex of species), MZUSP 24587, 5, 140–161, Brazil, Rio Acre; MNJR 4863, 1, 108, Brazil, Rio Madeira; SU 33386 (at CAS), 1, 93, Peru, Pebas; UMMZ 205085, 4, 98–146, and AMNH 40138, 2, 114–114, Bolivia, Río Marmore; ANSP 150171, 1, 95, Peru, Iquitos. USNM 124879, 2, 166–186, Río Ambiyacu; *Pimelodus blochi* DU-F-(JNB 90-78), 3, 85–103, Venezuela, Orinoco Delta region; DU-F-(JNB 47-78), 7, 68–200, Venezuela, Orinoco Delta region; DU-F-(JNB 95-79), 4, 96–143, Venezuela, Orinoco Delta region; *Pinirampus pirinampu* DU-F-(JNB 30-78), 1, 185, Venezuela, Orinoco Delta region.

Skeletal materials.—Following catalogue number, in parentheses, are number of specimens, type of preparation and standard length (or as indicated skull length) in mm, when available. Abbreviations for preparations of skeletal specimens: c&s—cleared and alizarin stained, diss—dissection, dry—dry skeleton, xr—radiograph.

Pimelodinae: Brachyplatystoma filamentosum DU F1052 (1, dry, ca. 220 skull length) Venezuela; DU F1079 (1, dry, ca. 200 skull length) Venezuela; DU F1080 (1, dry, ca. 200 skull length) Venezuela; *Brachyplatystoma juruense* DU F983 (1, dry, ca. 185) Venezuela; DU F1071 (1, dry, 590) Venezuela; MBUCV-V-ES13 (1, dry, 568) Venezuela; *Brachyplatystoma rousseauxi* DU F981 (1, dry, ca. 650) Venezuela; DU F1051 (1, dry, ca. 185 skull length) Venezuela; DU F1057 (1, dry, ca. 155 skull length) Venezuela; DU F1078 (1, dry, ca. 276 skull length) Venezuela; MBUCV-V-uncat. (1, dry, 132) Venezuela; MBUCV-V-uncat. (1, dry, ca. 270 skull length) Venezuela; *Brachyplatystoma vaillanti* DU F994 (dry), DU F1034 (1, dry, 370) Venezuela; MBUCV-V-CT235 (2, c&s, 114–116) Venezuela; MBUCV-V-uncat. (1, dry, 370)

Venezuela; *Calophysus macropterus* DU F985 (1, dry, 403) Venezuela; DU F1009 (1, c&s, 128) Venezuela; DU F1049 (1, dry, 217) Venezuela; DU F1103 (1, dry, 405) Venezuela; MBUCV-V-CT102 (1, c&s, 212); *Cheirocerus abuelo* MBUCV-V-CT1 (1, c&s, 154) Venezuela; *Exallodontus aguanai* DU F977 (1, dry, ca. 166) Venezuela; DU F865 (1, c&s, 82) Venezuela; DU F1047 (1, dry, ca. 186) Venezuela; DU F1048 (1, dry, ca. 72) Venezuela; *Duopalatinus peruanus* ANSP 160189 (1, c&s, 83) Venezuela; *Goslinia platynema* DU F992 (1, dry, ca. 415) Venezuela; DU F993 (1, dry, 182 skull length) Venezuela; DU F1076 (1, dry, ca. 561) Venezuela; MBUCV-V-CT443 (1, c&s) Venezuela; MBUCV-V-uncat (1, dry, 767) Venezuela; *Hemisorubim platyrhynchos* MBUCV-V-CT196 (1, c&s, 89) Venezuela; MCZ uncat. (1, dry) Brazil; *Hypophthalmus edentatus* DU F931 (1, dry, 352) Venezuela; DU F1043 (1, dry, 380) Venezuela; DU F1044 (1, dry, 390) Venezuela; MBUCV-V-uncat. (1, dry, 230) Venezuela; *Iheringichthys labrosus* DU F1000 (1, c&s, 86) Argentina; *Leiarius marmoratus* DU F987 (1, dry, ca. 320) Venezuela; DU F1036 (1, dry, 240) Venezuela; DU F1037 (1, dry, 210) Venezuela; DU F1053 (1, dry, 226) Venezuela; DU F1054 (1, dry, 276) Venezuela; DU F1055 (1, dry, 208) Venezuela; DU F1056 (1, dry, 293) Venezuela; MBUCV-V-CT234 (1, c&s, 52) Venezuela; *Megalonema* cf. *xanthum* DU F1011 (1, c&s, 72) Venezuela; DU F1001 (1, c&s, 72) Venezuela; *Megalonema* sp. DU F998 (1, c&s, 82) Venezuela; *Parapimelodus nigribarbis* MCP 6959 (1, c&s, 94) Brazil; *Parapimelodus valenciennes* MCP 12969 (1, c&s, 97) Venezuela; *Paulicea lutkeni* DU F982 (1, dry, 375) Venezuela; MBUCV-V-ES25 (1, dry, 260) Venezuela; *Perrunichthys perruno* MBUCV-V-14178 (1, diss) Venezuela; *Phractocephalus hemiliopterus* DU F925 (1, dry, 265) Venezuela; MBUCV-V-CT328 (1, c&s, 159), MBUCV-V-uncat. (3, dry, 415–ca. 800) Venezuela; *Pimelodina flavipinnis* DU F989 (1, dry, 310) Venezuela; DU F1008 (1, c&s, 107) Venezuela; *Pimelodus* sp. ("*altipinnis*") SU (at CAS) 54122 (1, dry, 35 skull length) Brazil; "*Pimelodus* A" (Orinoco) DU F1006 (1, c&s, 136) Venezuela; DU F1010 (1, c&s, 37) Venezuela; *Pimelodus altissimus* AMNH 40138 (1, c&s, 123) Bolivia; *Pimelodus blochi* DU F988 (3, dry, ca. 95–100) Venezuela; DU F1037 (1, dry, 210) Venezuela; DU F1077 (1, dry, ca. 214) Venezuela; DU-F1094 (1, dry, ca. 80) Venezuela; DU F1096 (1, dry, ca. 70) Venezuela; DU F1101 (1, dry, ca. 72) Venezuela; MBUCV-V-CT242, CT243, CT244, CT284 (11, c&s, 24–93) Venezuela; *Pimelodus coprophagus* MBUCV-V-CT150 (2, c&s) Venezuela; *Pimelodus grosskopfi* DU F919 (dry) Colombia; *Pimelodus ornatus* MBUCV-V-CT145 (2, c&s, 104–110) Venezuela; *Pimelodus pictus* DU F866 (c&s), MBUCV-V-CT70 (2, c&s, 60–67) Venezuela; DU F1012 (1, c&s, 65) Venezuela; *Pimelodus* cf. *clarias* DU F922 (1, dry, 212) Colombia; *P.* "*grosskopfei*" DU F919 (1, dry, 220) Colombia; *Pinirampus pirinampu* DU F984 (1, dry, 470) Venezuela; DU F1143 (11, c&s, 10–56) Venezuela; MBUCV-V-CT97, CT142 (3, c&s, 78–93) Venezuela; MBUCV-V-ES14 (2, dry, 310–572) Venezuela; *Platynematichthys notatus* MBUCV-V-uncat. (1, dry, 462) Venezuela; *Platysilurus* sp. DU F986 (1, dry, 186); DU F921 (1, dry, 230) Venezuela; MBUCV-V-CT92 (2, c&s, 86–102) Venezuela; *Platystomatichthys sturio* MBUCV-V-CT111 (1, c&s, 64) Venezuela; SU 22463 (at CAS) (1, dry, 96 skull length) Brazil; *Pseudoplatystoma faciatum* DU F864 (1, dry) Venezuela; DU F990 (1, dry, 970) Venezuela; DU F991 (1, dry, 258) Venezuela; DU F1060 (1, c&s, ca. 316) Venezuela; DU F1098 (1, dry, 215 skull length) Venezuela; DU F1100 (1, dry, ca. 395) Venezuela; DU F1125 (1, dry, ca. 240 skull length) Venezuela; MBUCV-V-CT489, CT491, CT492 (3, c&s, 25–66) Venezuela; MBUCV-V-ES17, uncat. (3, dry, 165–523) Venezuela; *Pseudoplatystoma tigrinum* DU F921 (1, dry, 230) Venezuela; DU F997 (1,

dry, 275 skull length) Venezuela; DU F1099 (1, dry, ca. 335) Venezuela; MBUCV-V-ES16 (1, dry, 557) Venezuela; MBUCV-V-CT uncat. (1, c&s, 25) Venezuela; *Sorubim lima* MBUCV-V-CT91, CT105, CT114 (2, c&s, 38–140) Venezuela; MBUCV-V-ES8 (4, dry, 195–226) Venezuela; *Sorubim* sp. DU F923 (1, dry, 336) Colombia; DU F1095 (1, dry, 195) Venezuela; *Sorubim* sp. MBUCV-V-uncat. (1, dry, ca. 500) Venezuela; *Sorubimichthys planiceps* MBUCV-V-CT505 (1, c&s) Venezuela; MBUCV-V-uncat. (1, dry, 265 skull length) Venezuela; *Steindachneridion parahybae* MCZ 25522 (1, dry) Brazil; MCZ 25523 (1, dry) Brazil.

Pseudopimelodinae: Lophiosilurus alexandri FMNH 95987 (1, c&s, 83) Brazil; *Microglanis poecilus* DU F1014 (3, c&s, 26–27) Venezuela; FMNH 9478 (4, c&s, 22–24) Venezuela; *Microglanis secundus* MBUCV-V-CT94 (3, c&s, 31–34) Venezuela; *Pseudopimelodus apurensis* DU F924 (1, dry, 430) Venezuela; DU F980 (1, dry, ca. 350) Venezuela; MBUCV-V-ES12 (1, dry, 418) Venezuela; DU-F1040 (1, dry, 285) Venezuela; *Pseudopimelodus raninus* MBUCV-V-CT95 (3, c&s, 58–72) Venezuela; *Pseudopimelodus* sp. DU F1102 (1, dry, ca. 75) Venezuela; *Pseudopimelodus* sp. MBUCV-V-CT222 (3, c&s, 30–52) Venezuela; *Zungaro zungaro* DU F920 (1, dry, 207) Colombia.

Rhamdiinae: Acentronichthys leptos FMNH 56902 (1, c&s, 37) Brazil; *Brachyglanis magoi* MBUCV-V-2600, CT139 (2, c&s, 48–50) Venezuela; MBUCV-V-uncat, (1, diss) Venezuela; *Brachyglanis melas* MBUCV-V-15919 (1, xr) Venezuela; *Brachyglanis* sp. AMNH 74394 (1, c&s) Venezuela; *Brachyrhamdia imitator* ANSP 139850 (2, c&s, 40) Venezuela; DU F1144 (2, c&s, 36–41) Venezuela; *Cetopsorhamdia picklei* MBUCV-V-CT98, CT138, CT264 (3, c&s, 56–65) Venezuela; *Cetopsorhamdia rosae* ANSP 137968 (c&s); *Cetopsorhamdia* sp. ROM ACC5056-RC86-42 (1, c&s, 49) Peru; *Chasmocranus longior* MBUCV-V-9817 CT137 (4, c&s, 28–56); *Chasmocranus* sp. DU F1005 (2, c&s, 22–25) Venezuela; DU F1002A (1, c&s, 27) Venezuela; ANSP 165353 (2, c&s, 57–58) Venezuela; *Gladioglanis conquistador* FMNH 94973 (5, c&s, 27–32) Ecuador; *Gladioglanis machadoi* DU F1001(1, c&s, 28), MBUCV-V-7293 (2, c&s, 23–26) Venezuela; FMNH 94793 (5, c&s, 20–28) Colombia; *Goeldiella eques* AMNH 13669 (c&s); *Heptapterus mustelinus* FMNH 56897 (1, c&s, 49) Brazil; *Heptapterus* sp. FMNH 83860 (1, c&s, 76); DU F1002B (1, c&s, 30) Venezuela; *Imparales panamensis* USNM 308587 (1, c&s, 54) Panama; *Imparfinis* sp. ANSP 135899 (c&s); ANSP 149927 (1, c&s, 43); *Imparfinis* sp. ROM ACC5056-RC86-31 (1, c&s, 62) Peru; *Leptorhamdia essequibensis* MBUCV-V-6959 (X); *Leptorhamdia* cf. *marmoratus* AMNH 74403 (c&s) Venezuela; *Medemichthys guayaberensis* ICN-NHM uncat. (2, c&s, 30–31) Colombia; *Myoglanis* sp. MBUCV-V-CT78 (1, c&s, 70) Venezuela; *Myoglanis* sp. AMNH 74407 (c&s); *Nannorhamdia nemacheir* DU F1004 (1, c&s, 25) Venezuela; USNM 121163 (1, c&s, 54) Venezuela; *Nannorhamdia pseudonemacheir* DU F1003 (3, c&s, 31–32) Venezuela; *Nannorhamdia* sp. MBUCV-V-14257 (1, c&s, 37) Venezuela; *Nannorhamdia* sp. MBUCV-V-14264 (1, c&s 49) Venezuela; *Nannorhamdia* sp. MBUCV-V-14346 (1, c&s, 34) Venezuela; *Nannorhamdia* sp. MBUCV-V-14464 (1, c&s, 32) Venezuela; *Nannorhamdia* sp. MBUCV-V-9215 (c&s); *Pariolius armillatus* ANSP 130596 (1, c&s, 35) Peru; *Pariolius fasciatus* ANSP 128696 (c&s); *Pariolius* sp. ANSP 178696 (2, c&s, 34–36); *Pimelodella chagresi* USNM 308586 (1, c&s, 82) Panama; *Pimelodella cristata* MBUCV-V-CT93, CT575, CT576 (4, c&s, 129–166) Venezuela; *Pimelodella hasemani* DU F1007 (3, c&s, 43–46) Venezuela; *Pimelodella metae* MBUCV-V-CT526, CT528 (3, c&s, 64–99) Venezuela; *Pimelodella* sp. DU F979 (1, dry, ca. 80) Venezuela; DU F1013 (1, c&s, 88) Venezuela; DU F1097 (2, dry, 55–92) Venezuela; DU F1104 (1, dry, 85) Venezuela; Rhamdiinae

gen. et sp. indet. MBUCV-V-9215 (1, c&s, 60) Venezuela; "*Pimelodus*" (cf *Brachyrhamdia*) *heteropleura* AMNH 52410 (2, c&s, 38); *Rhamdella* sp. MBUCV-V-CT190 (1, c&s, 119) Venezuela; USNM 270038 (c&s); *Rhamdia quelen* MBUCV-V-CT214, CT215, CT291, CT296 (7, c&s, 101–126) Venezuela; MBUCV-V-ES15 (3, dry, ca. 245) Venezuela; *Rhamdia sebae* DU F861 (1, c&s, 57) Venezuela; *Rhamdia wagneri* DU F1021 (1, dry, 204) Panama; *Rhamdia* sp. DU F978 (3, dry, ca. 95–100) Venezuela; *Rhamdia* sp. MBUCV-V-14048 (1, c&s) Venezuela; *Rhamdia* sp. USNM 270038 (1, c&s, 110) Venezuela.

Other siluriforms: Ageneiosidae: *Ageneiosus brevifilis* DU F927 (1, dry, 133) Venezuela; MBUCV-V-uncat. (1, dry, 350) Venezuela; *Ageneiosus ucayalensis* DU F928 (1, dry, 226) Venezuela; DU F1068 (1, dry, 316) Venezuela; *Ageneiosus* sp. DU F1145 (1, c&s, 60) Venezuela; Akysidae: *Acrocordontichthys melanogaster* FMNH 68010 (1, c&s, 38) Borneo; *Akysis* sp. UMMZ 214905 (1, c&s, 36) Vietnam; Amblycipitidae: *Amblyceps mangois* UMMZ 208651 (1, c&s, 35) Bangladesh; *Liobagrus andersoni* DU F1108 (2, c&s, 86–90) Korea; *Liobagrus formosanus* DU F1116 (1, c&s, 75) Taiwan; DU F1117 (1, c&s, 78) Taiwan; *Liobagrus mediadiposalis* DU F1109 (1, c&s, 82) Korea; DU F1111 (1, c&s, 83) Korea; *Liobagrus obesus* DU F1110 (2, c&s, 80–90) Korea; *Liobagrus xiurenensis* DU F1124 (1, c&s, 90) China; Amphiliidae: *Amphilius jacksoni* UMMZ 199987 (2, c&s, 32–85) Zambia; Ariidae: *Ariopsis seemani* DU Fl017 (1, dry, 243) Panama; DU F1019 (1, dry, 130) Panama; *Arius felis* DU F995 (1, dry, 175) North Carolina; *Arius jordani* DU F1020 (1, dry, 210) Panama; *Arius kessleri* DU F1015 (1, dry, 320) Panama; DU F1016 (1, dry, 165) Panama; *Arius proops* USNM 214860 (1, dry) Colombia; *Bagre panamensis* DU F1018 (1, dry, 210) Panama; *Potamarius nelsoni* UMMZ 143496 (1, dry) Guatemala; *Sciadops troscheli* USNM 214864 (1, dry) Colombia; Aspredinidae: *Agmus lyriformis* USNM 226079 (2, c&s, 56–62) Surinam; *Xyliphius* sp. DU F999 (1, dry, 64) Venezuela; *Bunocephalus* sp. DU F940 (1, dry, 94) aquarium spec.; Auchenipteridae: *Entomocorus benjamini* DU F1146 (2, c&s, 50–52) Venezuela; *Trachycorytes striatulus* SU (at CAS) 2151 (1, dry, 102) Brazil; Bagridae: *Bagroides malapterus* UMMZ 155695 (1, c&s, 87) Sumatra; *Bagrus ubangensis* SU (at CAS) 54218 (1, dry) Africa; *Chrysichthys furcatus* SU (at CAS) 54219 (1, dry) Africa; *Chrysichthys punctatus* SU (at CAS) 54220 (1, dry) Africa; *Chrysichthys walkeri* UMMZ 187901 (2, c&s, 57–65) Sierra Leone; *Coreobagrus ichikawai* UMMZ 187544 (1, c&s, 62) Japan; *Liocassis siamensis* UMMZ 186730 (2, c&s, 42–56) Thailand; *Mystus cavasius* UMMZ 186731 (1, c&s, 59) Thailand; *Mystus gulio* UMMZ 186724 (1, c&s, 55) Thailand; *Mystus nemurus* UMMZ 186685 (1, c&s, 50) Thailand; *Mystus vittatus* UMMZ 186780 (1, c&s, 63) Thailand; *Mystus wijcki* UMMZ 186785 (1, dry) Thailand; *Pelteobagrus nudiceps* UMMZ 187592 (1, dry, 166) Japan; *Pseudobagrus adiposalis* DU F1121 (1, c&s, 115) China; *Pseudobagrus aurantiacus* UMMZ 183870 (1, c&s, 65) Japan; Callichthyidae: *Corydoras* sp. DU F1147 (2, c&s, 38) Aquarium spec.; *Hoplosternum thoracatum* DU F1061 (1, dry, 169) Venezuela; DU F1062 (1, dry, 152) Venezuela; FMNH 84055 (2, c&s, 50–60) Colombia; *Hoplosternum littorale* MBUCV-V-ES003 (1, dry, ca. 250) Venezuela; Cetopsidae: *Cetopsis coecutiens* SU (at CAS) 54120 (1, dry) South America; *Paracetopsis occidentalis* SU (at CAS) 54120 (1, dry) Ecuador; Chacidae: *Chaca* sp. DU F1148 (1, dry, 80) Aquarium spec.; Clariidae: *Clarias batrachus* MBUCV-V-CT159 (1, c&s, 68) Venezuela; *Clarias gariepinus* UMMZ 200087 (1, dry, 300) Zambia; *Clarias ngamensis* UMMZ 200273 (2, dry, 258–279) Zambia; Cranoglanididae: *Cranoglanis multiradiatus* DU F917 (1, c&s, 56) China (PRC); Diplomystidae: *Diplomystes chilensis* MBUCV-V-CT585 (1, c&s) Chile; *Diplomystes papillosus* MCZ 8920 (1, c&s)

Chile; *Olivaichthys viedmensis* DU F913 (1, c&s, 115) Argentina; Doradidae: *Leptodoras* sp. DU F847 (1, c&s, 105) Venezuela; *Megalodoras iriwini* DU F925 (1, dry, 133) Venezuela; DU F996 (1, dry) Venezuela; DU F1041 (1, dry, 430) Venezuela; DU F1045 (1, dry, 440) Venezuela; DU F1069 (1, dry, ca. 345) Venezuela; DU F1126 (1, dry, 345) Venezuela; *Orinocodoras eigenmanni* DU F926 (1, dry, 198) Venezuela; *Platydoras costatus* DU F1105 (1, dry, 118) Venezuela; DU F1106 (1, dry, ca. 111) Venezuela; *Pseudodoras niger* DU F1092 (1, dry, 154 skull length) Venezuela; MBUCV-V-ES uncat. (1, dry, 170) Venezuela; *Pterodoras angeli* DU F1128 (1, dry, 83) Venezuela; MBUCV-V-ES uncat. (1, dry, 250) Venezuela; m spec.; Helogenidae: *Helogenes marmoratus* MBUCV-V-CT165 (2, c&s, 48–58) Venezuela; Heteropneustidae: *Heteropneustes fossilis* MBUCV-V-CT181 (1, c&s) India; †Hypsidoridae: †*Hypsidoris farsonensis* PU 20570, FMNH PF 10453 (1, fossil and cast, 169) Wyoming; Ictaluridae: *Ameiurus brunneus* DU F915 (2, dry, 139–145) North Carolina; DU F1137 (1, c&s, 59) North Carolina; UMMZ 186241-S4 (1, dry, 230) North Carolina; *Ameiurus catus* UMMZ 186242-S1 (1, dry, 287) North Carolina; *Amiurus melas* FMNH 42076 (2, c&s, 42–74) Illinois; UMMZ 189296-S1 (1, dry) Kansas; *Ameiurus natalis* DU F916 (2, c&s, 77–85) North Carolina; DU F1135 (1, c&s, 35) North Carolina; UMMZ 182060-S1 (1, dry, 228) Michigan; *Ameiurus nebulosus* DU F1129 (1, dry, 245) North Carolina; DU F1133 (1, c&s, 32) North Carolina; DU F 1138 (1, c&s, 63) North Carolina; UMMZ 182047-S1 (1, dry, 234) Michigan; *Ameiurus platycephalus* UMMZ 186254-S2 (1, dry, 202) South Carolina; *Ameiurus serracanthus* UMMZ 186258-S4 (1, dry, 180) Florida; †*Astephus antiquus* FMNH PF1035a,b (1, fossil, 71) Wyoming; USNM 8122 (1, fossil, 230) Wyoming; *Ictalurus furcatus* UMMZ 169031-S5 (1, dry, 327) Missouri; *Ictalurus punctatus* DU F930 (2, c&s, 50–51) North Carolina; DU F1081 (1, c&s, ca. 197) pond raised; UMMZ 186271 (1, dry, 304) Mississippi; DU F1131 (1, c&s, 43) North Carolina; DU F1134 (1, c&s, 42) aquarium; *Noturus flavus* UMMZ 126365 (1, dry, 224) Ohio; *Noturus furiosus* DU F1136 (2, c&s, 46–46) North Carolina; DU F 1139 (1, c&s, 62) North Carolina; *Noturus gyrinus* DU F 1132 (1, c&s, 50) North Carolina; *Noturus insignis* DU F 1130 (2, c&s, 40–45) North Carolina; DU F1140 (1, c&s, 73) North Carolina; DU F1141 (1, c&s, 66) North Carolina; DU F1142 (2, c&s, 30–32) North Carolina; DU F 1143 (5, c&s, 94–110) North Carolina; *Noturus stigmosus* UMMZ 165841-S1 (1, dry, 87) Michigan; *Prietella phreatophila* UMMZ 173788 (1, c&s) Mexico; *Pylodictis olivaris* UMMZ 169029 (1, dry, 306) Missouri; *Satan eurystomus* Hubbs and Bailey: WMM (Witte Memorial Museum) 34-20-7, G (1, xr, 69) Texas; *Trogloglanis pattersoni* SIOH 51-379-18A (1, c&s) Texas; Loricariidae: *Acanthicus histrix* DU F1093 (1, dry, ca. 420) Venezuela; *Loricaria* sp. DU F1066 (1, dry, 263) Venezuela; DU F1127 (2, dry, 175–195) Venezuela; *Panaque* sp. DU F1067 (1, dry, 242) Venezuela; *Sturisoma* sp. DU F1064 (1, dry, ca. 294) Venezuela; DU F1065 (1, dry, 215) Venezuela; Malapteruridae: *M. electricus* MBUCV-V-CT335 (1, c&s, 65) Africa; USNM 118777 (1, c&s, 79) Liberia; *Malapterurus microstoma* USNM 265121 (1, dry, 520) Aquarium spec.; Mochokidae: *Atopocheilus* sp. CAS 47458 (1, dry) Africa; *Euchilichthys* sp. SU (at CAS) 54221 (1, dry) Africa; *Synodontis longirostris* SU (at CAS) 54222 (1, dry) Africa; *Synodontis membranaceous* MBUCV-V-CT171 (1, c&s) Africa; Nematogeneidae: *Nematogenys inermis* Guichenot IUM 15060 (1, c&s) Chile; Olyridae: *O. longicaudata* UMMZ 208811 (1, c&s, 85) Bangladesh; *Olyra* sp. CAS 54502 (1, c&s, 54) Thailand; Pangasiidae: *Pangasius* sp. DU F907 (1, dry, 250) Thailand; Plotosidae: *Plotosus canius* UMMZ 155790 (1, dry, 255) Indonesia; Schilbeidae: *Eutropius congensis* SU (at CAS) 54135 (1, dry, 195) Zaire; *Helicopha-*

gus waandersi UMMZ 186797 (2, c&s, 77–117) Thailand; *Laides hexanema* UMMZ 186798 (1, c&s, 65) Thailand; *Schilbe mystus* MBUCV-V-174 (1, c&s) Africa; UMMZ 187334 (1, dry) Uganda; UMMZ 200118 (1, dry, 305) Zambia; Siluridae: *Belodontichthys dinema* DU F-906 (1, dry, 370) Thailand; *Hemisilurus mekongensis* DU F-904 (1, dry, 422) Thailand; *Kryptopterus bicirrhis* DU F-912 (1, c&s, 42) aquarium specimen; *Parasilurus asotus* DU F-908 (1, dry, 320) China; DU F-929 (1, c&s, 130) No data; *Parasilurus grahami* DU F-911 (1, dry, 382) China; *Silurus cochinchinensis* DU F-909 (1, c&s, 93) No data; DU F-910 (1, c&s, 93) No data; *Wallago attu* DU F905 (1, dry, 506) Pakistan; Sisoridae: *Bagarius bagarius* UMMZ 186793 (1, c&s, 90) Thailand; *Erethistes pusillus* UMMZ 208697 (1, c&s, 36) Bangladesh; *Gagata cenia* UMMZ 208281 (1, c&s, 41) Bangladesh; UMMZ 208356 (1, c&s, 46) Bangladesh; *Glyptothorax ribeiroi* UMMZ 208955 (1, c&s, 26) Bangladesh; *Glyptothorax shawi* UMMZ 208967 (1, c&s, 24) Bangladesh; *Glyptothorax trilineatus* UMMZ 186849; *Hara hara* UMMZ 208748 (1, c&s, 50) Bangladesh; *Hara jerdoni* UMMZ 208401 (1, c&s, 20) Bangladesh; Trichomycteridae: *Trichomycterus* sp. FMNH 96618 (1, c&s, 104) Ecuador.

Acknowledgments

We are especially indebted to Don Stewart for sharing with us his knowledge of research resources and taxonomy of pimelodid catfishes, and to Genie Böhlke for providing Figure 8. For providing specimens and access to facilities we thank Jonathan Baskin, Dave Canatella, Barry Chernoff, Bill Eschmeyer, Carl Ferraris, Karsten Hartel, Hector López, Naercio Menezes, Susan Jewett, Antonio Machado-Allison, Doug Nelson, Francisco Provenzano, Lucia Py-Daniel, Ramiro Royero, Bill Saul, Scott Schaeffer, Don Stewart, and Richard Vari. Alan Bornbusch, Don Stewart, Stan Weitzman, John Friel and Xiaoping Chen provided helpful comments and suggestions on the manuscript.

Much support for this work came from the National Science Foundation through grants DEB 77-14439 and DEB 80-22343. We acknowledge use of R/V *Eastward* operated by Duke University; the Duke National Oceanographic Facility was supported in 1978 and 1979 by NSF, CG-00005. Support for JGL to travel to Venezuela in connection with this study came from the United States Information Service's Council for the International Exchange of Scholars through an American Republics Research Grant and from the Duke University Research Council. Support for FML and PN to study pimelodid catfishes was provided by the Venezuelan Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICIT), Proyecto SI-1500.

Literature Cited

Arratia, G. 1987. Description of the primitive family Diplomystidae (Siluriformes, Teleostei, Pisces): morphology, taxonomy and phylogenetic implications.—Bonner Zoologische Monographien, No. 24:1–120.

Bleeker, P. 1862. Atlas ichthyologique des Indes Orientales Neerlandaises. Tome II. Silurodes, Chacoides et Heterobranchoides. J. Smith and Gide, Amsterdam, The Netherlands.

Böhlke, J. E. 1970. A new species of the doradid catfish genus *Leptodoras,* with comments on related forms.—Proceedings of the California Academy of Sciences, 4th ser., 38(3):53–62.

Bornbusch, A. H. 1988. Phylogenetic studies of the silurid catfishes (Teleostei: Siluriformes). Unpublished Ph.D. dissertation, Duke University, 524 pp.

Driver, C. S. 1919. On the Luciopimelodinae, a new subfamily of the South American Siluridae.—Proceedings of the American Philosophical Society 58:448–456.

Eigenmann, C. H., & W. R. Allen. 1942. Fishes of western South America. The University of Kentucky, Lexington. 1–494.

———, & R. S. Eigenmann. 1888. Preliminary notes on South American Nematognathi, I.—Proceedings of the California Academy of Sciences 1:1–509.

———, & ———. 1890. A revision of the South American Nematognathi or cat-fishes.—Occasional Papers of the California Academy of Sciences 1:1–509.

Ferraris, C. J., Jr. 1988. Relationships of the neotropical catfish genus *Nemuroglanis,* with a description of a new species (Osteichthys: Siluriformes: Pimelodidae).—Proceedings of the Biological Society of Washington 101:509–516.

Fink, S., & W. Fink. 1981. Interrelationships of the ostariophysan fishes (Teleostei).—Zoological Journal of the Linnaean Society 72(4):297–358.

Gill, T. N. 1872. Arrangement of the families of fishes or classes Pisces, Marsipobranchii, and Leptocardii.—Smithsonian Miscellaneous Collections 11(2):1–45.

Grande, L. 1987. Redescription of *Hypsidoris farsonensis* (Teleostei: Siluriformes), with a reassessment of its phylogenetic relationships.—Journal of Vertebrate Paleontology 7:24–54.

Günther, A. 1864. Catalogue of fishes in the British Museum. 5, London, 1–455.

Howes, G. H. 1983. Problems in catfish anatomy and phylogeny exemplified by the Neotropical Hypophthalmidae (Teleostei: Siluroidei).—Bulletin of the British Museum (Natural History), Zoological Series 45(1):1–39.

———, & G. G. Teugels. 1989. Observations on the ontogeny and homology of the pterygoid bones in *Corydoras paleatus* and some other catfishes.—Journal of Zoology 219(3):441–456.

Lacépède, B. G. 1803. Histoire naturelle des poissons V. Paris, Plassan.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

López-Rojas, H., J. G. Lundberg, & E. Marsh. 1985. Design and operation of a small trawling apparatus for use with dugout canoes.—North American Journal of Fisheries Management 4(3): 331–334.

Lundberg, J. G. 1975. Homologies of the upper shoulder girdle and temporal region bones in catfishes (Order Siluriformes), with comments on the skull of the Helogeneidae.—Copeia 1975: 66–74.

———, & C. Stager. 1985. Microgeographic morphological variation in the Venezuelan knifefish *Eigenmannia macrops* (Gymnotiformes, Sternopygidae).—Environmental Biology of Fishes 13(3):173–181.

———, & F. Mago-Leccia. 1986. A review of *Rhabdolichops* (Gymnotiformes, Sternopygidae), a genus of South American freshwater fishes, with descriptions of four new species.—Proceedings of the Academy of Natural Sciences of Philadelphia 138(1):53–85.

———, & L. A. McDade. 1986. On the South American catfish *Brachyrhamdia imitator* Myers (Siluriformes, Pimelodidae), with evidence for a large intrafamilial lineage.—Academy of Natural Sciences of Philadelphia, Notula Naturae. 463:1–24.

———, A. H. Bornbusch, & F. Mago-Leccia. 1991. *Gladioglanis conquistador* n. sp. (Siluriformes: Pimelodidae) from Ecuador and diagnoses of two subfamilies, Rhamdiinae and Pseudopimelodinae.—Copeia 1991:190–209.

———, O. Linares, M. E. Antonio, & P. Nass. 1988. *Phractocephalus hemiliopterus* (Pimelodidae, Siluriformes) from the upper Miocene Urumaco Formation, Venezuela: a further case of evolutionary stasis and local extinction among South American fishes.—Journal of Vertebrate Paleontology 8:131–138.

Mago-Leccia, F., J. G. Lundberg & J. N. Baskin. 1985. Systematics of the South American fish genus *Adontosternarchus* (Gymnotiformes, Apteronotidae).—Contributions in Science, Natural History Museum of Los Angeles County No. 358: 1–19.

Mees, G. F. 1974. The Auchenipteridae and Pimelodidae of Suriname (Pisces, Nematognathi).—Zoologische Verhandlingen 132:1–256.

Regan, C. T. 1911. The classification of the teleostean fishes of the order Ostariophysi. Siluroidea.—Annals and Magazine of Natural History. Ser. 8, 8:553–577.

Schultz, L. P. 1944. The catfishes of Venezuela with a description of 44 new forms.—Proceedings of the United States National Museum 94(3172): 173–338.

Stewart, D. J. 1985. A new species of *Cetopsorhamdia* (Pisces: Pimelodidae) from the Río Napo Basin of Eastern Ecuador.—Copeia 1985:339–344.

———. 1986a. Revision of *Pimelodina* and description of a new genus and species from the Peruvian Amazon (Pisces, Pimelodidae).—Copeia 1986:653–671.

———. 1986b. A new pimelodid catfish from the deep channel of the Río Napo, eastern Ecuador (Pisces: Pimelodidae).—Proceedings of the Academy of Natural Sciences of Philadelphia 138:46–52.

———, & S. Pavlik. 1985. Revision of *Cheirocerus* (Pisces: Pimelodidae) from tropical freshwaters of South America.—Copeia 1985:356–367.

(JGL) Department of Zoology, Duke University, Durham, North Carolina 27706, U.S.A. (FML, PN) Instituto de Zoología Tropical, Universidad Central de Venezuela, Apartado 59058, Caracas 1041A, Venezuela.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 870–877

THE IDENTITY AND TAXONOMIC STATUS OF *MEGAPODIUS STAIRI* AND *M. BURNABYI* (AVES: MEGAPODIIDAE)

David W. Steadman

Abstract.—*Megapodius stairi* and *M. burnabyi* were described by Gray (1861) on the basis of single eggs collected, respectively, in areas of Samoa and Tonga where no megapodes have been recorded since. For more than a century, both names have been regarded as synonyms of *M. pritchardi* Gray (1864), an extant species known from whole specimens as well as eggs. An examination of both holotypical eggs reveals that neither *M. stairi* or *M. burnabyi* is unequivocally synonymous with *M. pritchardi,* with *M. stairi* particularly unlikely to represent *M. pritchardi.* On the basis of size and color, I cannot rule out that these specimens represent *M. freycinet* or perhaps even an extinct species of *Megapodius. Megapodius stairi* and *M. burnabyi* are best regarded as *nomina dubia,* mainly because their holotypical specimens lack species-specific characters.

The To'aga archaeological site on Ofu Island, American Samoa, recently yielded a fragmentary ulna and femur of an indeterminate species of megapode (*Megapodius* sp.), providing the easternmost record for the entire family Megapodiidae (Steadman 1991). The bones from To'aga are larger than those of *M. pritchardi* (confined to Niuafo'ou, Tonga), the only species of megapode that survives east of Vanuatu (=New Hebrides) and *M. laperouse* of Palau and the Mariana Islands. They are much smaller, however, than the bones of two extinct species recently described from late Holocene archaeological and paleontological sites: *M. alimentum* from the Tongan islands of Lifuka and 'Eua; and *M. molistructor* of New Caledonia and Lifuka (Balouet & Olson 1989; Steadman 1989a, 1989b, pers. obs.). The archaeological bones of *M. freycinet* from Tikopia, Solomon Islands (Steadman et al. 1990), and those from the To'aga site are at the smallest end of the size range of *M. freycinet,* a widespread and geographically variable species (sensu Mayr 1938, who unites within *freycinet* several species recognized by Peters 1934) that reaches its modern eastern limit in Vanuatu, about 2100 km west of Ofu. Except for the Tikopia record, *M. freycinet* has not been recorded prehistorically from islands outside of its modern range. Probable records from the 19th and early 20th centuries, however, suggest a much greater past than present distribution for *M. freycinet* (see Discussion).

The To'aga specimens of *Megapodius* represent the first well documented record of a megapode from Samoa. There is, however, historical evidence that a megapode may have existed in the mid-1800s in Western Samoa, as well as in central Tonga. This paper reviews that evidence as part of an effort to determine the natural distribution of megapodes in Oceania.

Review of the Evidence

Gray (1859:46) listed the following record from the collections of the British Museum: "Megapodius _____? The egg only of a *Megapodius* has been brought from the Samoan or Navigator' Islands; but no example of the perfect bird has yet been recorded by

naturalists or others as from that locality." Two years later, Gray (1861:290) named the Samoan megapode as *Megapodius stairi,* describing its egg as "dusky white. Length 3″ 1‴, width 1″ 1‴. Samoan or Navigator's Islands (Rev. J. B. Stair 1847)." [″ = inch; ‴ = a line = $\frac{1}{12}$ inch.] *Megapodius stairi* was listed without further comment by Gray (1864). Gray (1861:290) described a second new species, *Megapodius burnabyi,* also known from a single egg, this one collected sometime before 1861 by Lt. Burnaby, R.N., at an undetermined island in the Ha'apai Group of Tonga. (In the 19th century, Ha'apai was variously known as Hapai, Hapace, Harpace, or Hapache.) The holotypical eggs of *M. stairi* and *M. burnabyi* are in the British Museum (Natural History), the former catalogued as BM(NH) 1847.10.11.5 and the latter, which was not entered in the registry until three years ago, as 1988.4.3.

The habits of a megapode on the Tongan island of Niuafo'ou were described in some detail by Bennett (1862), who collected a single egg (BM(NH) 1863.5.16.3). Bennett believed that the megapode from Niuafo'ou would be found to be conspecific with *M. freycinet* of Vanuatu. The megapodes on Niuafo'ou were named *Megapodius pritchardi* by Gray (1864), with a skin designated as the holotype. Finsch & Hartlaub (1867: xxxvi, xxxvii, 153–155) recognized *M. pritchardi* and questioned the validity of *M. stairi* and *M. burnabyi.* Hutton (1869:353) noted, "We have also in the [Auckland] Museum what is probably a new species of Megapode, from Niupo [=Niuafo'ou], one of the islands in the Friendly group [=Tonga]." Buller (1870:15) noted that *M. stairi* "is not yet placed on the list of well-determined species," and proposed the name *Megapodius huttoni* based on the specimen (a skin) mentioned by Hutton (see also Salvin 1872:418). Beginning with Finsch (1877), *M. huttoni* has been regarded as a synonym of *M. pritchardi.*

Finsch (1872:33) listed *Megapodius stairi* as being from Samoa and stated that (p. 52; translated from German), "The *Megapodius* of the Samoan Islands unfortunately remains unknown." Whitmee (1875:447), who regarded *M. stairi* as a synonym of *M. pritchardi,* stated that "The type of *M. stairii* was, I believe, *sent* from Samoa, but was *brought here* from the island of Nina-fou, where *M. pritchardi* exists. If I am correct in this, then the former name has the right of precedence." Of *M. stairi,* Layard (1876: 496) stated, "Mr. Whitmee and Mr. Krause both assured me no Megapode exists in the Navigators' Islands [=Samoa]. Mr. Whitmee affirmed that the bird on which the species was founded was brought from Ninafoo by the Rev. W. Stair, and transmitted to England among some Samoan skins; hence the mistake." Of *M. burnabyi,* Layard (1876:503) noted, "No megapode is found in the group [Tonga], according to the testimony of the whites, who, however, know the Ninafoo bird well." Thus ornithologists began to doubt the validity of *Megapodius stairi* and *M. burnabyi,* at least in part because no further evidence of megapodes had come forth from Samoa or Ha'apai.

Finsch (1877), who listed *Megapodius pritchardi* Gray 1864, and *M. burnabyi* Gray 1861 as synonyms of *M. stairi,* stated (p. 784), "Since Mr. Layard assures us that *M. stairi,* Gray, was based on specimens from Ninafu (and not from Samoa, where no Megapode exists) the older name must be applied to this species." Layard's assurance was based upon the belief of Whitmee and Krause that the holotypical egg of *M. stairi* came from Niuafo'ou rather than Samoa. The basis of this belief is uncertain, although it may be due to the fact that entire specimens of megapodes had been found only on Niuafo'ou. It is possible, however, that when the single eggs were sent by Rev. Stair in 1847 and by Lt. Burnaby before 1861, megapodes existed in Samoa and Ha'apai, where they are now extinct.

The original, hand-written data slip with the holotype of *Megapodius burnabyi* notes

that this egg was "called the 'chief's egg' as they are only allowed to eat them." Bennett (1862:247) noted that the nesting grounds of *M. pritchardi* on Niuafo'ou were "under the protection of the king or chief, and by his permission only can the birds or eggs be procured." Because the consumption of megapodes and their eggs was limited, it is reasonable to speculate that these birds were rare and probably prestigious items for trade. Megapodes and their eggs may have been exchanged as items in the extensive trading network that operated among Fiji, Tonga, and Samoa in late prehistoric and early historic times (Stair 1895; Kirch 1984:238–242, 1988:257–260). Even if megapodes of the Fiji/Tonga/Samoa region were confined by that time to Niuafo'ou, they would have been known to Tongans in Ha'apai, as well as to Samoans. Evidence that the holotypes of *M. stairi* and *M. burnabyi* might have been transported to Samoa and Ha'apai from Niuafo'ou would require that the specimens be sufficiently similar to eggs of *M. pritchardi* to consider the three names synonymous, a matter to be addressed shortly.

Wiglesworth (1891:58) united the three named species as *Megapodius stairi,* giving Niuafo'ou as the only locality. Oates (1901) followed Finsch (1877) and Wiglesworth (1891) in synonymizing the three species, but merged them under the later name *Megapodius pritchardi,* stating (p. 17) that "The eggs of Pritchard's Megapode are subject to much variation, being reddish-brown, pinkish, stone-coloured, brown or whitish. They measure from 2.95 to 3.15 in length, and from 1.6 to 1.9 in breadth." Lister (1911) reviewed the distribution of *Megapodius* without mentioning *M. stairi* or *M. burnabyi,* and concluded (p. 758) that, "there is no satisfactory evidence that a Megapode has ever existed on any Pacific island east of a line bordering the Philippines, Solomon Islands, and New Hebrides except the Pelews, Marianne Islands, and Niuafou." His statement marked the disappearance of *M. stairi* and *M. burnabyi* from the ornithological literature until their brief mention by Walters (1980:33), Balouet & Olson (1989: 11), and Steadman (1989b). Neither name was noted in the reviews of Pacific megapodes by Peters (1934), Mayr (1938, 1945), or Amadon (1942).

The length and width of the holotypical egg of *Megapodius stairi* was given incorrectly by Gray (1861:290) as 3″ 1‴ and 1″ 1‴ (78 × 28 mm when converted from inches and lines to metric). For his species *M. pritchardi,* which included *M. stairi* and *M. burnabyi,* Oates (1901) gave measurements of 75–80 × 41–48 mm. Six eggs of *M. pritchardi* found on Niuafo'ou in 1984 measured 73.2–76.4 × 41.1–44.5 mm (Rinke 1986).

My measurements of *Megapodius* eggs are presented in Table 1. The holotypes of *M. stairi* and *M. burnabyi* are 78.8 × 47.6 mm and 77.3 × 43.9 mm, respectively. For *M. stairi,* the length is greater than in 69 of 70 eggs of *M. pritchardi,* while the width is greater than in 71 of 72 eggs of that species. Compared to *M. freycinet layardi* of Vanuatu (the extant population of megapodes nearest to *M. pritchardi*), both the length and width of *M. stairi* are well within the range of variation. For *M. burnabyi,* the length is greater than in 64 of 70 eggs of *M. pritchardi* and less than in 41 of 47 eggs of *M. freycinet layardi,* while the width is near the mean of *M. pritchardi* and less than 46 of 47 eggs of *M. f. layardi.* Thus in measurements *M. stairi* from Samoa more closely resembles *M. freycinet* (*M. f. layardi* or perhaps *M. f. eremita*) than *M. pritchardi,* while *M. burnabyi* from Ha'apai resembles *M. pritchardi* slightly more than *M. freycinet.* Because *M. pritchardi* was once more widespread (I have just discovered its bones on 'Eua, Tonga), the surviving population on Niuafo'ou may not represent the full range of egg size in this species.

Unfortunately, color is not a reliable species-level character in eggs of *Megapodius* because of the great amount of variation in specimens. Weir (1973:81) described the

eggs of *M. pritchardi* as "light brown in color occasionally having scattered white flecks. The eggs tend to lighten with age but this is not a reliable indicator of age since there is a great variation in color at the time of laying." Rinke (1986:83) reported fresh eggs of *M. pritchardi* as "yellowish ochre." Coates (1985:140) noted that the originally buff colored egg of *M. freycinet* "is said to turn coffee brown after a few days in the mound." The holotype of *M. stairi* is a creamy buff with slight mottling, while that of *M. burnabyi* is a darker, slightly mottled olive tan. I have seen both of these colors in eggs of *M. pritchardi* as well as *M. freycinet.* To summarize, I found no consistent differences between the eggs of *M. pritchardi* and *M. freycinet* in color, surface texture, proportions, or overall shape.

The exact islands on which the holotypes of *Megapodius stairi* and *M. burnabyi* were collected have not been determined. As stated by Gray (1861), the holotype and only specimen of *M. stairi* was collected in "Samoa" in 1847 by Reverend John B. Stair (1815–1898), a missionary and natural historian who lived in what now is called Western Samoa (Wynne 1969:200). His botanical collections indicate that Stair was on the island of Upolu in 1843 (Anon. 1925:727; Bridson et al. 1980:233), whereas his own writings (Stair 1895) suggest that he lived on Upolu as well as the neighboring island of Savai'i in the 1840's. Thus it seems likely that the holotype of *M. stairi* was collected either on Upolu or Savai'i, rather than on the smaller, eastern Samoan islands of Tutuila and the Manu'a Group. As far as I can determine from the British Museum collections, the holotype of *Megapodius stairi* is the only egg known to have been collected by Stair. Each of the British Museum skins collected by Stair lists merely "Samoa" rather than a specific island as the collection locality.

Lt. (later Captain) M. B. Burnaby, R.N. (1825–1896; Anonymous 1897:694; Pine 1952:310) collected the holotype of *Megapodius burnabyi* in the Ha'apai Group of Tonga before 1861. I am aware of no other natural history specimens collected by Burnaby. Because the island of Lifuka was (and still is) the center of population and commerce within the Ha'apai Group, it is likely that Burnaby's ship was anchored at Lifuka when he obtained the megapode egg destined to bear his name.

Summary and Discussion

The 19th century oological holotypes of *Megapodius stairi* and *M. burnabyi* still exist and indeed represent megapodes. *Megapodius stairi* was collected in Samoa, probably on Upolu or Savai'i, while *M. burnabyi* was collected in the Ha'apai Group of Tonga, probably on Lifuka. No specimens or other records of megapodes have been collected subsequently in Samoa or Ha'apai. On the basis of size, the holotype of *M. stairi* may be conspecific with *M. freycinet,* a widespread species that reaches its eastern limit today in Vanuatu. The single egg of *M. stairi* is larger than 99% of modern specimens of *M. pritchardi,* which is known from wild populations only on Niuafo'ou (Tonga), an island between Upolu and Ha'apai. The holotype of *M. burnabyi* is of a size that might pertain to either *M. freycinet* or *M. pritchardi.* Either or both of the holotype eggs of *M. stairi* and *M. burnabyi* may have been inter-island trade items of 19th century Samoans and Tongans. If *M. stairi* represents a megapode more closely related to, or conspecific with, *M. freycinet,* then *M. stairi* may represent the same species as the archaeological bones of an indeterminate megapode from Ofu, which also are at the lower limit of the size range of *M. freycinet* but larger than *M. pritchardi.*

Considering the vulnerability of megapodes on many oceanic islands (Olson 1980; Balouet & Olson 1989; Steadman 1989a, 1989b) and the great amount of inter-island trade in late prehistory in the Tonga-Samoa-Fiji region, the holotypical eggs of

Table 1.—Measurements (in mm) of the eggs of *Megapodius,* with mean, range, and sample size; mainly from specimens in the British Museum (Natural History), supplemented by those in the American Museum of Natural History, New York State Museum, and National Museum of Natural History, Smithsonian Institution.

	Locality	Length	Width
M. stairi, holotype	Samoa: probably Upolu or Savai'i	78.8	47.6
BM(NH) 1847.10.11.5		1	1
M. burnabyi, holotype	Tonga: Ha'apai: probably Lifuka	77.3	43.9
BM(NH) 1988.4.3		1	1
M. pritchardi	Tonga: Niuafo'ou	74.8	44.4
		71.4–79.7	40.4–49.0
		70	72
M. freycinet layardi	Vanuatu: Tanna, Santo, Tongoa,	81.8	47.4
	Malakula, Efate, Banks	71.5–89.7	42.6–50.8
		47	47
M. freycinet eremita	Solomon Is.: Choiseul, San Cristo-	78.0	47.8
	bal, Isabel, Treasury, Guadal-	73.5–84.4	43.9–51.4
	canal, Savo, Gulf, Arnavon	47	50
M. freycinet eremita	Bismark Arch.: Feni, Nissan, New	76.9	47.5
	Britain, Lihir	71.3–79.8	44.4–50.0
		17	17
M. freycinet affinis	Papua New Guinea	80.4	49.9
		78.8–82.5	46.5–52.1
		3	3
M. freycinet duperryii	Papua New Guinea	85.5	52.6
		80.1–90.8	49.2–54.9
		10	10
M. freycinet macgillivrayi	Papua New Guinea: Rossell, Fer-	81.2	53.0
	gusson Islands	79.7–83.5	51.9–55.0
		7	7
M. freycinet macgillivrayi	Papua New Guinea: Trobriand Is.	88.2	54.2
		83.7–93.2	51.2–55.7
		6	6
M. freycinet yorki	Australia: Queensland	88.7	53.6
		84.4–96.0	50.8–55.6
		11	11
M. freycinet tumulus	Australia: Northern Territory	88.7	54.8
		86.1–93.4	52.8–57.4
		9	9
M. freycinet buruensis	Moluccas: Buru	79.4	48.9
		75.5–83.4	44.7–50.8
		6	7
M. freycinet reinwardt	Indonesia: Tiga, Megalun	74.4	46.5
		72.1–75.7	45.5–47.9
		3	3
M. freycinet reinwardt	Indonesia: Komodo, Kalao	84.3	51.2
		83.0–86.4	50.4–52.0
		3	3
M. freycinet gilberti	Indonesia: Sulawesi	79.7	50.5
		1	1
M. freycinet tabon	Philippines: Mindanao	80.2	48.9
		73.6–89.5	43.9–54.1
		44	44
M. freycinet pusillus	Philippines: Luzon	81.6	48.5
		1	1

Table 1.—Continued.

	Locality	Length	Width
M. freycinet pusillus or *M. f. tabon*	Philippines: island unknown	80.3 75.9–85.0 7	48.8 46.6–50.8 7
M. freycinet cumingi	Borneo, Palawan	76.5 71.9–80.1 8	47.1 45.9–48.4 8
M. freycinet nicobariensis	Nicobar Is.: northern island(s)	82.1 76.4–88.7 77	52.4 49.0–55.5 77
M. freycinet abbotti	Nicobar Is.: Great Nicobar	83.4 81.2–85.3 4	50.3 49.7–51.6 4
M. freycinet abbotti or *M. f. nicobariensis*	Nicobar Is.: island unknown	81.4 78.5–84.4 9	52.5 49.1–54.6 9
M. cf. *freycinet* subsp.?	Andaman Is.	80.3 77.3–84.1 4	50.3 48.3–52.0 5
M. laperouse senex	Palau: island unknown	77.7 72.4–83.4 7	46.4 44.5–47.8 7

Megapodius stairi and *M. burnabyi* might represent valued trade items that originated on some other island that still supported megapodes in the 19th century. If the largest eggs tended to be chosen for chiefly consumption or trade, then even *M. stairi* is likely to be synonymous with *M. pritchardi,* known historically only from Niuafo'ou but recorded as a fossil from 'Eua (pers. obs.). That *M. stairi* and *M. burnabyi* may be synonymous with *M. pritchardi* is reasonable geographically, as Niuafo'ou is directly between Ha'apai and Western Samoa and must have been visited regularly by trading boats from Tonga and Samoa.

If conspecific, the names *Megapodius stairi* Gray 1861 and *M. burnabyi* Gray 1861 would both have priority over *M. pritchardi* Gray 1864. Gray (1861) named both *M. stairi* and *M. burnabyi* on p. 290, with the former several lines above the latter. As neither of these named species is unequivocally synonymous with *M. freycinet* or *M. pritchardi,* I recommend that they be considered *nomina dubia* and the name *M. pritchardi* therefore should be retained for the species on Niuafo'ou. Unless additional evidence is forthcoming, neither *M. stairi* or *M. burnabyi* should be regarded as certain records of indigenous populations of megapodes in 19th century Samoa or Ha'apai. The survival of *M. pritchardi* on Niuafo'ou has been due to chiefly control of the exploitation of eggs and birds from the conspicuous nest mounds. The people of Niuafo'ou realized that conserving the megapodes, which probably occurred nowhere else in the region, would help to sustain their share of commerce in the Samoa-Tonga-Fiji trade network.

If *Megapodius stairi* and *M. burnabyi* represent populations indigenous to the islands where their holotype eggs were collected, they are not the sole examples of megapodes that survived into the 19th or early 20th century only to disappear before an adult skin could be collected. Eggs, downy chicks, or written evidence suggest the former pres-

ence of megapodes, certainly or probably in the size range of *M. freycinet,* on the following islands: New Caledonia (*M. "andersoni"*; see Balouet & Olson 1989:11); the Kermadec Islands (Lister 1911); Lord Howe Island (two downy chicks in British Museum, examined by DWS in 1990; Lister 1911: 758, claims that these specimens are really from "New Hope" Island, another name for Niuafo'ou; I regard the matter as unresolved); and the Andaman Islands (five eggs in British Museum, examined in 1990 by DWS; see Table 1). In each case, bones (yet to be discovered) may be our only hope to learn more about these and other lost populations of megapodes.

Acknowledgments

This research was supported in part by National Science Foundation grant BSR-8607535. I thank T. L. Hunt and P. V. Kirch for inviting me to study the bird bones from To'aga. G. Petri and F. E. Warr assisted in library research. S. L. Olson and M. P. Walters shared information on specimens of megapodes. For comments on the manuscript, I thank R. C. Banks, M. R. Browning, P. V. Kirch, N. G. Miller, S. L. Olson, and M. P. Walters.

Literature Cited

Amadon, D. 1942. Birds collected during the Whitney South Sea Expedition. XLIX. Notes on some non-passerine genera, 1.—American Museum Novitates 1175:1–11.

Anonymous. 1897. The Navy List. Her Majesty's Stationary Office, London.

———. 1925. Catalogue of the printed books and pamphlets in the library of the Linnean Society of London. Turnbull & Spears, Edinburgh.

Balouet, J. C., & S. L. Olson. 1989. Fossil birds from late Quaternary deposits in New Caledonia.—Smithsonian Contributions to Zoology 469: 1–38.

Bennett, G. 1862. [Letter from Dr. G. Bennett on *Didunculus, Tallegalla,* and *Megapodius.*].—Proceedings of the Zoological Society of London 1862:246–248.

Bridson, G. D. R., V. C. Phillips, & A. P. Harvey. 1980. Natural history manuscript resources in the British Isles. Mansell, London, 473 pp.

Buller, W. 1870. Notice of a species of Megapode, in the Auckland Museum.—Transactions of the New Zealand Institute 3:14–15.

Coates, B. J. 1985. The birds of Papua New Guinea, vol. I. Dove Publications, Alderly, Queensland, 464 pp.

Finsch, O. 1872. Zur ornithologie der Samoa-Inseln.—Journal für Ornithologie 20:30–58.

———. 1877. On a collection of birds from Niuafou Island, in the Pacific.—Proceedings of the Zoological Society of London 1877:782–787.

———, & G. Hartlaub. 1867. Beitrag zur fauna Centralpolynesiens. Ornithologie der Viti-, Samoa- und Tonga-Inseln. Halle, Germany.

Gray, G. R. 1859. Catalogue of the birds of the tropical islands of the Pacific Ocean, in the collection of the British Museum. British Museum, London, 72 pp.

———. 1861 [pub. April 1862]. List of species composing the Family Megapodiidae, with descriptions of new species, and some account of the habits of the species.—Proceedings of the Zoological Society of London 1861:288–296.

———. 1864. On a new species of megapode.—Proceedings of the Zoological Society of London 1864:41–44.

Hutton, F. W. 1869. [Letter from the Auckland Museum.].—Ibis, new ser., 5:352–353.

Kirch, P. V. 1984. The evolution of the Polynesian chiefdoms. Cambridge University Press, Cambridge, 314 pp.

———. 1988. Niuatoputapu: the prehistory of a Polynesian chiefdom.—Thomas Burke Memorial Washington State Museum Monograph 5, 287 pp.

Layard, E. L. 1876. Notes on the birds of the Navigators' and Friendly islands, with some additions to the ornithology of Fiji.—Proceedings of the Zoological Society of London 1876:490–506.

Lister, J. J. 1911. The distribution of the avian genus *Megapodius* in the Pacific islands.—Proceedings of the Zoological Society of London 1911:749–759.

Mayr, E. 1938. Birds collected during the Whitney South Sea Expedition. XXXIX. Notes on New Guinea birds. IV.—American Museum Novitates 1006:1–16.

———. 1945. Birds of the Southwest Pacific. The Macmillan Co., New York, 316 pp.

Oates, E. W. 1901. Catalogue of the collection of birds' eggs in the British Museum (Natural History), vol. I. British Museum (Natural History), London, 245 pp.

Olson, S. L. 1980. The significance of the distribution of the Megapodiidae.—Emu 80:21–24.

Peters, J. L. 1934. Check-list of birds of the world, vol. II. Harvard University Press, Cambridge, Massachusetts, 401 pp.

Pine, L. G. (ed.). 1952. Burke's genealogical and heraldic history of the landed gentry, 17th ed., 3 vols. Burke's Peerage Ltd., London.

Rinke, D. 1986. Notes on the avifauna of Niuafo'ou Island, Kingdom of Tonga.—Emu 86:82–86.

Salvin, O. 1872. Index to the ornithological literature of 1871.—Ibis, third ser., 2:413–468.

Stair, J. B. 1895. Floatsam and jetsam from the great Ocean; or, summary of early Samoan voyages and settlements.—Journal of the Polynesian Society 4:99–131.

Steadman, D. W. 1989a. Extinction of birds in Eastern Polynesia: a review of the record, and comparisons with other Pacific island groups.—Journal of Archaeological Science 16:177–205.

———. 1989b. New species and records of birds (Aves: Megapodiidae, Columbidae) from an archeological site on Lifuka, Tonga.—Proceedings of the Biological Society of Washington 102: 537–552.

———. 1991. Birds from the To'aga site, Ofu, American Samoa: prehistoric loss of seabirds and megapodes. University of California, Berkeley, Archaeological Research Facility Contributions (in press).

———, D. S. Pahlavan, & P. V. Kirch. 1990. Extinction, biogeography, and human exploitation of birds on Tikopia and Anuta, Polynesian outliers in the Solomon Islands.—Occasional Papers of the Bishop Museum 30:118–153.

Walters, M. P. 1980. Megapodiidae. P. 33 *in* Complete birds of the world. David & Charles, North Pomfret, Vermont.

Weir, D. G. 1973. Status and habits of *Megapodius pritchardi*.—Wilson Bulletin 85:79–82.

Whitmee, S. J. 1875. List of Samoan birds, with notes on their habits &c.—Ibis, third ser., 5:436–447.

Wiglesworth, L. W. 1891. Aves Polynesiae. A catalogue of the birds of the Polynesian subregion (not including the Sandwich Islands).—Abhandlungen und Berichte des Königlischen zoologischen und anthropologisch-ethnographischen Museums zu Dresden 6:1–92.

Wynne, O. E. 1969. Biographical key—names of birds of the world—to authors and those commemorated. Col. E. O. Wynne, Courtwood, Sandlehearth, Fordingbridge, England, 246 pp.

Biological Survey, New York State Museum, The State Education Department, Albany, New York 12230, U.S.A.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 878–891

THE SKULL OF THE EOCENE *TRIODON ANTIQUUS* (TRIODONTIDAE; TETRAODONTIFORMES): SIMILAR TO THAT OF THE RECENT THREETOOTH PUFFERFISH *T. MACROPTERUS*

James C. Tyler and Colin Patterson

Abstract.—The fossil record of the tetraodontiform family Triodontidae previously has been based only on jaw bones. All of these elements are from the early and middle Eocene, and include: numerous unfused premaxillae and fused dentaries for the more commonly recorded *Triodon antiquus* Leriche from several localities in Europe and one in North America; two fused dentaries for *T. cabindensis* Leriche from Africa; and a single dentary for *T. macrognathus* Taverne & Nolf from Belgium. In a monograph on tetraodontiform osteology and relationships, Tyler (1980:260) noted that the presence of *Triodon*-like jaw parts in the Eocene tells us nothing about what the fish behind the jaws was like, and that there was no guarantee that the general form of even the better known *T. antiquus* was at all like that of the only Recent species of the family, the threetooth pufferfish *T. macropterus*. The recovery in 1982 of a specimen of *T. antiquus* from the Lower Eocene London Clay with both the upper and lower jaws attached to a relatively complete skull, along with the cleithra and pelvis, indicates that this Eocene species is similar to the Recent species, especially in the distinctive shapes of the hyomandibular, subopercle, and cleithrum. Examination of a smaller specimen of *Triodon macropterus* than previously available reveals the presence of a posttemporal, a bone thought to be present among tetraodontiforms only in the Balistoidei but lost in the Triodontidae and all of the other Tetraodontoidei.

The family Triodontidae is of special interest because it is clearly the most primitive extant group within the Tetraodontoidei, the more advanced of the two lineages of tetraodontiforms (here and elsewhere, higher categories sensu Tyler 1980). Based on both osteology (Tyler 1962, 1980) and myology (Winterbottom 1974), the Triodontidae is considered the sister group of all of the other tetraodontoid families—the Tetraodontidae, Diodontidae, Molidae, and Eocene Eoplectidae. Triodontids retain many of the primitive features of the Balistoidei, the other major tetraodontiform lineage, including a spiny dorsal fin (although rudimentary and sometimes absent), pelvis, urohyal, dorsal roof of the myodome, complete scapular foramen, a knob on the scapula for support of the uppermost pectoral-fin ray, unsutured actinosts, 12 caudal-fin rays, a generalized caudal skeleton and branchial basket, etc. However, triodontids possess the single most important tetraodontoid synapomorphy—which is the presence of highly modified, non-protruding teeth fully incorporated into the matrix of the premaxillae and dentaries, together forming a complex beak-like structure supported by a massive and firmly sutured palatine-ethmoid-vomerine block.

The Recent Species of *Triodon*

A single species of triodontid is alive today: *T. macropterus* Lesson, benthic in the

Indo-western Pacific from southeast Africa to Japan in depths of 50 to 300 meters (Tyler 1967:90, Kyushin et al. 1977:364, Matsuura 1985:409, Smith 1986:894). The great majority of specimens in museum collections are relatively large adults of between 285 and 480 mm SL (Tyler 1967:90), with a few specimens recorded as large as 540 mm SL (Smith 1986:894) and 550 mm SL (Gloerfelt-Tarp & Kailola 1984:293). Specimens smaller than 285 mm SL have only rarely been reported, such as in Winterbottom (1974:5) for 270 mm SL and in Burgess & Axelrod (1974:1357) for 224 mm SL specimens [the illustration of the 487 mm SL = BL or body length specimen described by Kyushin et al. 1982:299 is incorrectly labeled 103 mm BL; K. Amaoka and K. Matsuura, pers. comm.].

However, trawling by the R/V *Soela* in 1986 off the coast of Queensland, Australia, has procured five relatively small specimens of *T. macropterus* of 89 to 103 mm SL, from depths of 216 to 228 meters. These latter specimens from the Australian Museum are relevant to this study because they are of about the same size as that extrapolated for the Eocene skull of *T. antiquus* described here, allowing comparison of the osteology of fossil and Recent specimens of similar size. This reveals at least one feature not previously known in *T. macropterus.*

The Fossil Species of *Triodon*

The first described and best known fossil triodontid is *T. antiquus* Leriche (1905:170; description and illustrations repeated with only slight modification in Leriche 1906: 266; and further noted in Leriche 1908:3), based only on several premaxillae and dentaries from the early and middle Eocene (Ypresian, Lutetian) of Belgium and France. The teeth were described as small and incisiform, and arranged in superimposed rows incorporated into the substance of the jaw bones, as is the case in both triodontids and diodontids. While the dentaries are fully fused together in the midline, as in both triodontids and diodontids, the premaxillae are separate, a combination unique to the triodontids. Six premaxillae and ten dentaries of *T. antiquus* were illustrated. One of the dentaries (Leriche 1905, pl. 12, fig. 31) is relatively more elongate (lesser width between the posterolateral rami and more acutely angled at the anteromedial point of the beak) than the others and was given the varietal name *elongatus.* Leriche noted that these Eocene jaw bones are all far smaller than those found in any of the large adult specimens of the Recent *T. macropterus* then available in museum collections, which were about 300 to 400 mm SL. For example, Leriche's illustrated premaxillae of *T. antiquus* are between 11 and 15 mm greatest length and the dentaries between 9 and 12 mm greatest width between the posterolateral rami (anguloarticular processes), whereas in a 391 mm SL specimen of *T. macropterus* the premaxillae are 40 mm long and the dentaries 37 mm wide (this specimen, ANSP 98917, was described and illustrated by Tyler 1980:255, fig. 182, and has been reexamined for this work). Of the five young adult specimens of *T. macropterus* that have become available at the Australian Museum, the 103 mm SL specimen (AMS 25802-006) has been cleared and stained. The premaxillae are 11 mm long and the dentaries 10 mm wide, these figures being at the lower end of the range of these measurements in *T. antiquus.* By extrapolation from the 103 mm SL specimen of *T. macropterus,* the premaxillae and dentaries of *T. antiquus* described by Leriche represent young adult specimens of about 93 to 140 mm SL.

Casier (1946:175) somewhat increased our knowledge of *T. antiquus* by briefly describing and illustrating it on the basis of 24 dentaries and 3 premaxillae from the early Eocene (Ypresian) of Belgium. These jaw bones were even smaller than those described by Leriche, with the illustrated premaxillae being about 5 mm long and the

dentaries between about 3 and 8 mm wide. By extrapolation from the 103 mm SL specimen of *T. macropterus,* these premaxillae and dentaries represent juveniles and young adults of about 31 to 82 mm SL.

Given his familiarity with *T. antiquus,* the report by Casier (1966:374) that this species is absent from the London Clay Formation (Ypresian) of southern England simply indicates that specimens of it had not yet been collected from that formation. We now know that detached dentaries of *T. antiquus* are not uncommon there (see Material), even though a relatively complete skull such as reported here is a rarity.

Some years after his original description of *T. antiquus,* Leriche (1919:480, name only; 1920:85, description and illustration) described *T. cabindensis* on the basis of a single large dentary from the middle Eocene (Lutetian) of Angola at Sassa Zao, Cabinda. The greatest width of this dentary, including an estimate of the missing left posterolateral region, is about 30 mm. The dentary of *T. cabindensis* was said to be relatively wider than in *T. antiquus* and to have the small teeth that are incorporated into the bone lamelliform rather than incisiform. The individual teeth of *T. cabindensis* were illustrated as being about 1.5 mm in width and having about five distinct lobes along the upper edge (toward the mouth). By extrapolation from the 391 mm SL specimen of *T. macropterus,* the type dentary of *T. cabindensis* represents a large adult of about 317 mm SL. A second large dentary of *T. cabindensis,* also of about 30 mm width, was listed, briefly described, and illustrated by Dartevelle & Casier (1943:91, 1949:253, 1959, pl. 20, fig. 2) from Landana, Cabinda, from the same horizon as the holotype from Sassa Zao.

This additional specimen of *T. cabindensis* became the subject of a detailed and extensively illustrated description and comparison to the holotype dentary of *T. cabindensis* and to the premaxillae and dentaries of *T. antiquus* by Casier (1960:33–37, pl. 2, figs. 5a–5i), who referred to the additional specimen as "cf. *cabindensis.*" Casier noted a number of superficial and internal differences between the dentaries from Sassa Zao and Landana in the size, form, and ornamentation of the individual teeth in the exposed outer surface of the bone and in the internal trituration plate, and of their relationships with the bony material of the dentary. He found even greater differences between these two large dentaries from Cabinda and the much smaller dentaries of *T. antiquus* from Belgium. He not only questioned whether the dentary from Landana was conspecific with that from Sassa Zao, but, especially since only dentaries were known, whether both were the remains of diodontids rather than triodontids (Casier 1960:35–37).

The only other described species that has been referred to *Triodon* is *T. macrognathus* Taverne & Nolf (1978:147). These authors had two dentaries from the middle Eocene (Lutetian) Lede Formation of Belgium, one of which they referred to *T. antiquus.* The other they described as the new species *T. macrognathus* because of the lesser ornamentation of small individual teeth on the external surface of the beak, the stronger posterolateral wings, and a more slender and distinctly less prominent beak. The illustrations of these two dentaries indicate that the small individual teeth apparent on the outer surface of the dentary in *T. antiquus* are absent in *T. macrognathus,* but the supposed differences in the shape and size of the dentaries are not particularly distinctive to us. The dentary shown for *T. antiquus* is about 5 mm greatest width, and that for *T. macrognathus* about 6 mm wide, corresponding by extrapolation from the 103 mm SL specimen of *T. macropterus* to specimens of, respectively, 52 and 62 mm SL. We remain skeptical about whether the difference between these two dentaries is adequate for specific recognition. Nolf (1970:

113) had previously listed "*Triodon* cf. *antiquus*" from reworked Eocene fossils in the Pleistocene of Merelbeke, Belgium.

The only report of *T. antiquus* from other than Europe is the description and illustration by Weems & Horman (1983:45) of a dentary from the early Eocene (Ypresian) Nanjemoy Formation in Maryland, U.S.A. This dentary is about 10 mm greatest width (as it is also from the anterior midline to the rear of the posterolateral rami) and has small individual teeth with only slightly crenulated upper edges on the outer surface of the beak and several pairs of large trituration teeth internally. These features are all typical of the European specimens of *T. antiquus,* including the type material, which is of similar size to the Maryland dentary (Weems & Horman were mistaken in thinking the Maryland dentary to be larger than most of the European material). The 103 mm SL specimen of *T. macropterus* has a dentary width of 10 mm, and the Maryland dentary thus represents a specimen of *T. antiquus* of very similar size. Weems & Horman (1983:47) noted that the Maryland dentary has a beak that is about as long as wide, whereas in European *T. antiquus* the beak tends to be somewhat wider than long, giving the Maryland beak an especially angular appearance. By contrast, they pointed out that the dentary of *T. cabindensis* is extremely wide (as is that of *T. macrognathus,* a species of which they were not aware). Weems & Horman (1983) were appropriately cautious in their interpretation of the differences in proportions between their Maryland dentary and most European materials of *T. antiquus,* stating that in light of the "highly variable nature of the dentition in figured specimens of *T. antiquus,*" the Maryland dentary "is not truly distinctive when based on only a single specimen," and that "unless enough material becomes available to allow a statistical comparison [by size] between the European and American populations," variants like the Maryland dentary are "best referred to the highly variable *Triodon antiquus.*" We have examined the Maryland dentary and fully support that conclusion.

The new skull of *Triodon* described below and illustrated in Figs. 1–5 is from the Lower Eocene (Ypresian) London Clay Formation. It was collected on the foreshore at Sheppey, Kent, in 1982 by Mr. Brian Gasson of Redhill, Surrey, and was presented by him in 1984 to the British Museum (Natural History). The premaxillae and dentary of this skull, although much abraded, have all the essential characteristics in size and shape and in the form of the exposed tooth structures (e.g., only slight crenulation of the upper edge of the small outer teeth) of the European jaws referred to *T. antiquus,* and we are confident that it represents the same species.

Description of the Skull of *Triodon antiquus* Leriche, 1905

The skull as recovered was in a rounded nodule with flat sides (Fig. 1), in which the roof of the cranium, ethmoid-lateral ethmoid-vomerine region, premaxilla, dentary, quadrate, opercular bones, cleithrum and basal region of the pelvis were exposed, affording sufficient clues to its identity as *Triodon antiquus.* Removal of the clay matrix from the right side and top of the skull has exposed the bones of the cheek and snout (Figs. 2–4) and presents further confirmation of the identification, while also indicating the great similarity between the Eocene *T. antiquus* and the Recent *T. macropterus.* The major bones that have been lost from the skull of the London Clay specimen are the frontals, maxillae, articulars, and angulars (and all bones of the pectoral girdle except the cleithra).

The measurements of the skull are: 40 mm from front of upper jaw to rear of supraoccipital (excluding the supraoccipital crest that is abraded away); 35 mm from

Fig. 1. *Triodon antiquus,* BM(NH) P.62702, length from front of upper jaw to rear of supraoccipital 40 mm, left side of skull in matrix as recovered, Lower Eocene, London Clay Formation, Sheppey, Kent. Rule is mm.

front of ethmoid-vomerine block to rear of supraoccipital; 17 mm greatest width across pterotics-posttemporals (edge estimated on posterolaterally incomplete right side); 11 mm greatest width between the posterolateral rami of dentary; 11 mm greatest midline length of dentary (between mid-front of dentary and a line across posterior ends of rami); 11 mm from mid-front of dentary to posterolateral edge of dentary. Two comparable measurements from the 103 mm SL specimen of *T. macropterus* allow for the estimation of the length of the London Clay specimen; 34 mm from the front of the ethmoid-vomerine block to the rear of the supraoccipital (exclusive of the posterior extention of the crest), and 10 mm greatest width between the posterolateral rami of the dentary. By extrapolation from these figures, the London Clay specimen was between 106 and 111 mm SL.

The osteology of the Recent *T. macropterus* previously has been known only on the basis of large adults, especially the two cleared and stained specimens described by Tyler (1962:795, 1980:244, see Tyler 1967: 88 for a review of specimens then available for study, including older skeletal materials used by Camille Dareste and Henri Hollard in the mid-19th century). Because the skull of *T. antiquus* from the London Clay obviously represents a much smaller individual than the 391 and 463 mm SL specimens of *T. macropterus* described and extensively illustrated in the literature, we have taken advantage of the recent availability of relatively small specimens of *T. macropterus* at the Australian Museum to clear and stain a 103 mm SL specimen and illustrate dorsal and lateral views of its skull (Fig. 6) for ease of comparison with our reconstructions of the Eocene skull (Fig. 5).

Fig. 2. *Triodon antiquus,* same specimen as Fig. 1, right side of skull with matrix removed. See Fig. 5 for interpretation of bones.

On the dorsal surface of the neurocranium the most clearly delineated bone is the supraoccipital, whose crest is abraded down to its base. The lines of articulation are less clear between the anterodorsal extension of the exoccipital where it separates the supraoccipital from the epiotic, posttemporal, and pterotic. The frontals, which in the Re-

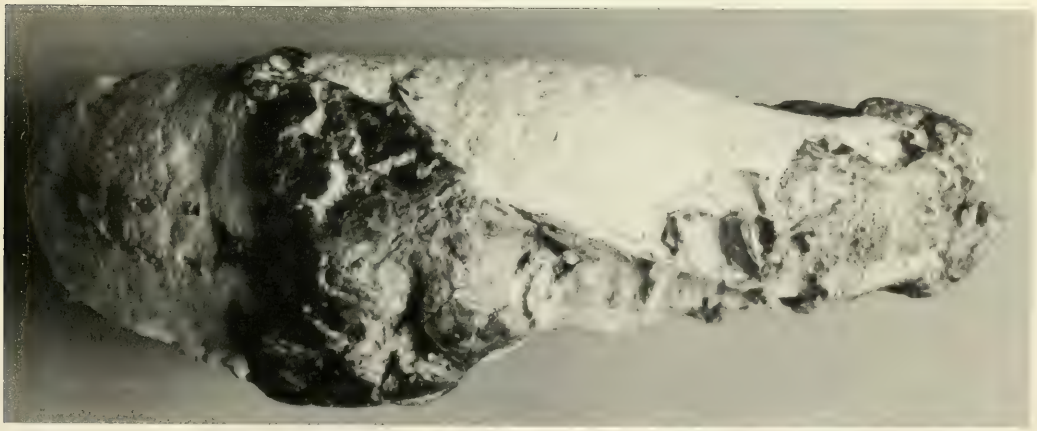


Fig. 3. *Triodon antiquus,* same specimen as Fig. 1, slightly oblique dorsal view of skull with matrix removed from right side. See Fig. 5 for interpretation of bones.

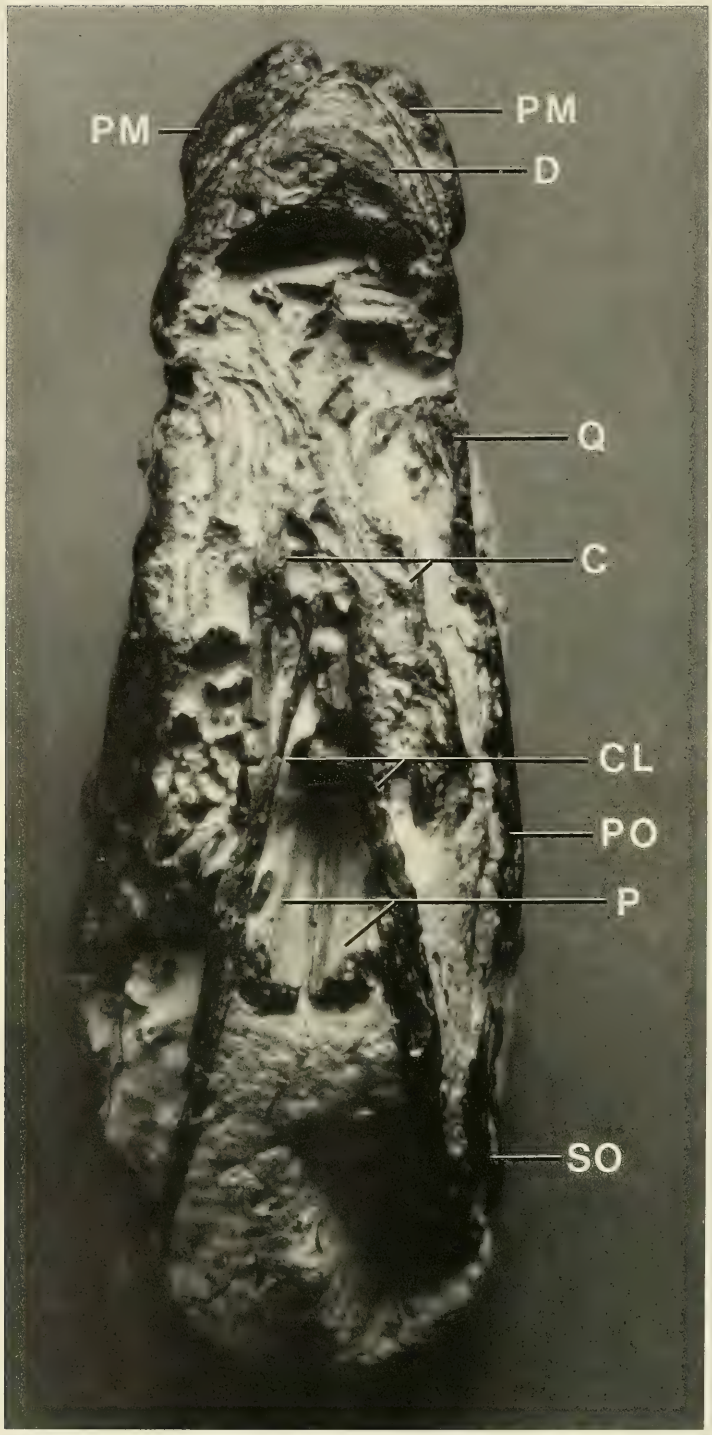


Fig. 4. *Triodon antiquus,* same specimen as Fig. 1, ventral view of skull. See legend for Fig. 6 for explanation of abbreviations of names of bones.

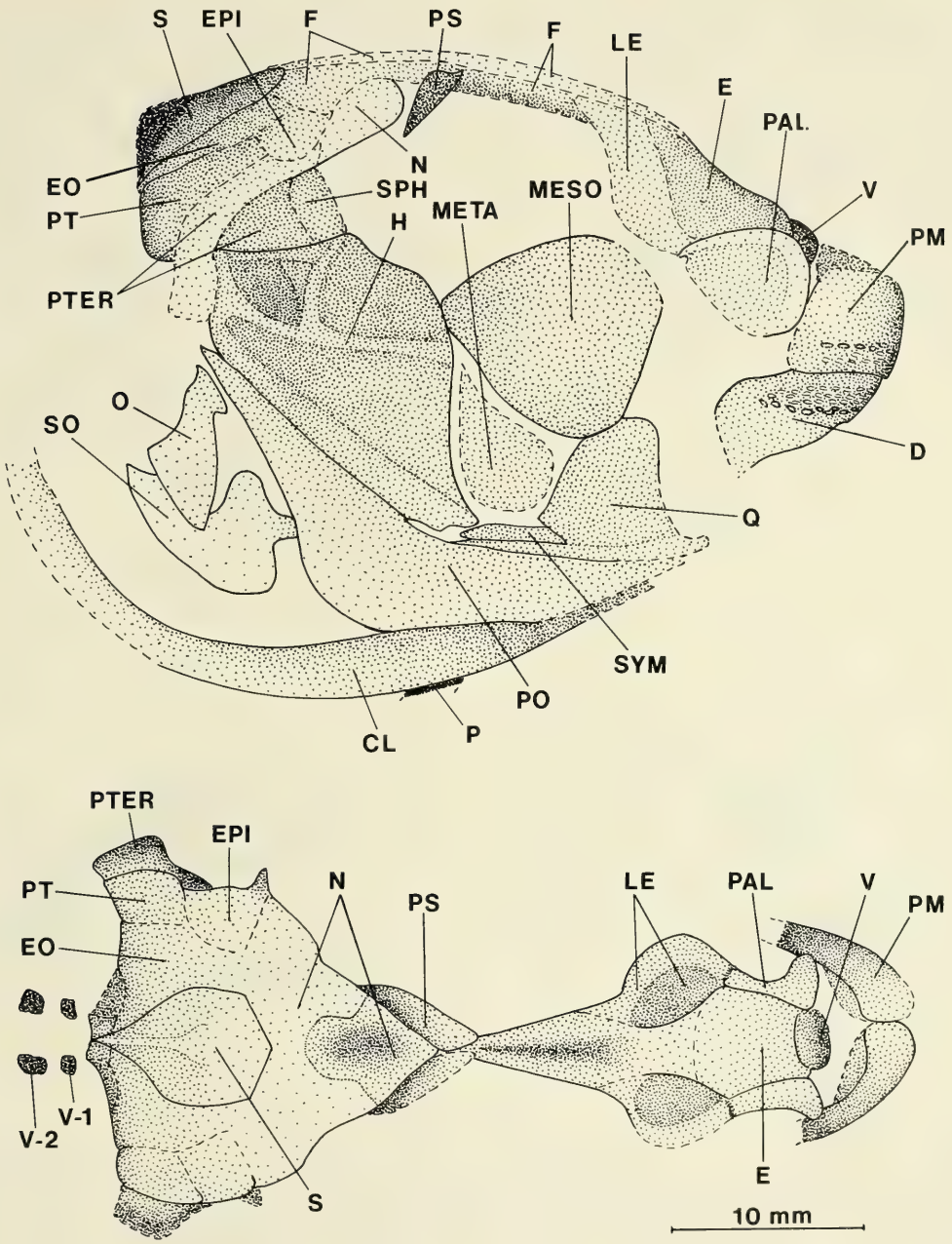


Fig. 5. *Triodon antiquus,* same specimen as Fig. 1, reconstruction of right lateral (above) and dorsal surfaces of skull (frontals missing). See legend for Fig. 6 for explanation of abbreviations of names of bones.

cent species slightly overlie the anterior edge of the supraoccipital, exoccipitals, and epiotics, are both missing. The region of the neurocranium underlying the frontals appears to be more heavily pyritized from the level of the front of the supraoccipital, epiotics, and exoccipitals to the pterosphenoids, while between the pterosphenoids and

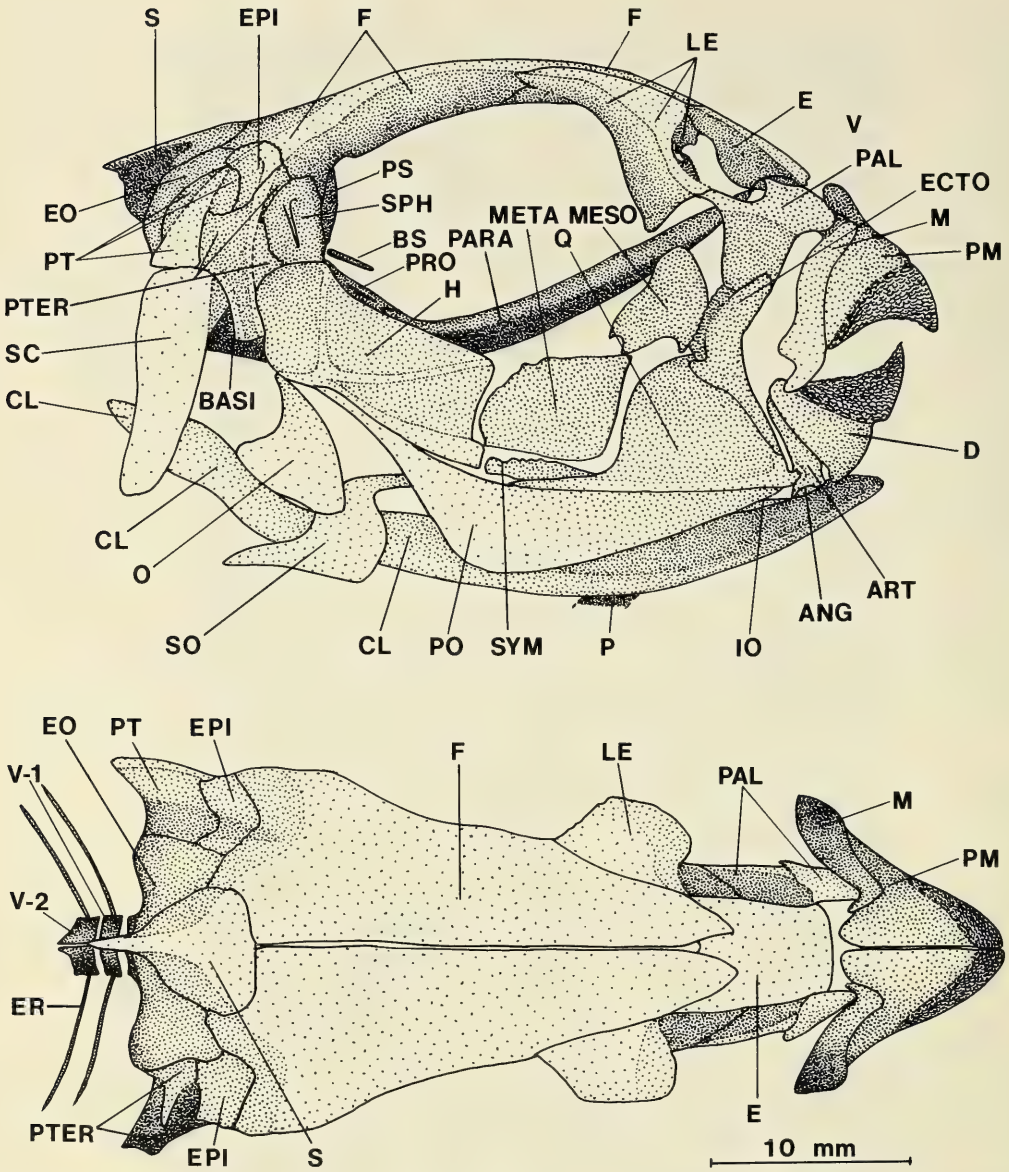


Fig. 6. *Triodon macropterus*, AMS I 25802-006, 103 mm SL, Queensland, Australia, right lateral (above) and dorsal views of skull (with posttemporal on right side removed in the dorsal view to expose the underlying pterotic. Abbreviations for the names of bones: ANG—angular; ART—articular; BO—basioccipital; BS—basisphenoid; C—coracoid; CL—cleithrum; D—dentary; E—ethmoid; ECTO—ectopterygoid; EO—exoccipital; EPI—epiotic; ER—epipleural rib; F—frontal; H—hyomandibular; IO—interopercle; LE—lateral ethmoid; M—maxilla; MESO—mesopterygoid; META—metapterygoid; N—neurocranium; O—opercle; P—pelvis; PAL—palatine; PARA—parasphenoid; PM—premaxilla; PO—preopercle; PRO—prootic; PS—pterosphenoid; PT—posttemporal; PTER—pterotic; Q—quadrate; S—supraoccipital; SC—supracleithrum; SPH—sphenotic; SO—subopercle; SYM—symplectic; V—vomer; V1—1st vertebra; V2—2nd vertebra.

the lateral ethmoids the mineralization probably is the impression of the ventromedial orbital flanges of the absent frontals. The massive ethmoid is relatively clearly indicated anteromedially on the skull, lateral to which are strong lateral ethmoids. At the lower anterior end of the ethmoid the anterior region of the underlying vomer can be seen, more so than is the case in *T. macropterus,* but probably mainly because of abrasion of the overlying ethmoid and the angle of view of the skull rather than any substantive difference between it and the Recent species.

Both premaxillae are much abraded, especially posterolaterally, and the medial region of the left premaxilla also is much worn away. However, it is clear that the premaxillae were separate bones, although closely articulated in the midline. The deeper parts of the articular area between the two premaxillae are not well enough exposed to determine if the articulation was strengthened by interdigitating bony processes from the apposed medial surfaces, as is the case in the Recent species of *Triodon* and of tetraodontids. A few individual small tooth elements are incorporated into the matrix of the bone of the premaxilla, but these teeth are better preserved in the dentary. The dentary is fully fused across the midline into a single piece with a gentle u-shaped curve along the internal edge but more acute along the front of the beak.

On the exposed external surface of the dentary the individual small teeth are clearly evident, being oblong with a slightly crenulated upper edge. This slight crenulation may be slightly better developed in *T. antiquus* than in the Recent species, but the teeth are much less crenulated than the deeply notched small teeth described for *T. cabindensis* (these small teeth are not apparent in *T. macrognathus*). The developmental centers for the individual small teeth form a row along the lower edge of the external tooth surface, as they do also on the premaxillae. Much of the internal anteromedial surface of the dentary can be seen in ventral view, and the rear edges of a pair of large laterally elongate trituration teeth are evident. All of the jaw structures in the London Clay specimen are essentially similar to those of the Recent *T. macropterus.*

At the rear of the skull the condyle formed by the exoccipitals for articulation with the first vertebra is evident. The first several vertebrae are indicated by the much abraded left and right sides of the neural arches, the neural spines having been completely worn away.

Laterally on the skull the bones of the hyomandibular and opercular series are especially clear. The hyomandibular is large and strong. It bears a distinctive horizontal crest for muscle attachment. Another crest courses vertically upward from the horizontal crest to the anterior region of the place of articulation of the hyomandibular with the pterotic and sphenotic laterally (and presumably with the prootic internally), almost exactly as in the Recent *T. macropterus.* This size, shape, and pattern of crests is unique among tetraodontiforms, although many diodontids and some molids, but not tetraodontids, among the tetraodontoids also have large and variously crested hyomandibulars (see illustrations throughout Tyler 1980). Another bone of relatively distinctive shape in both the London Clay skull of *T. antiquus* and in the Recent *T. macropterus* is the subopercle. It has a prominent anterior process from its anterior edge to behind the upper posterior edge of the preopercle where in the Recent species it connects by ligament to the posterior end of the interopercle. Such an anterior process is found among other tetraodontiforms only in diodontids and, in a more modified form, molids and is one of the few ways in which diodontids and molids are more similar to triodontids than are tetraodontids (Tyler 1980:342). The anterior process of the subopercle in *T. antiquus* differs from that in

T. macropterus by having its origin in about the middle of the anterior edge, rather than from the dorsal end as in *T. macropterus,* diodontids and, less clearly, molids.

Anteroventral to the hyomandibular the symplectic and the rear portion of the quadrate are clear. The articular and angular and the front end of the right quadrate are missing, leaving a large gap on this side between the posterolateral ramus of the dentary and the area of articulation with the quadrate. However, the anterior end of the quadrate is exposed in the matrix on the unprepared left side of the skull, and it has the typical triodontid (and tetraodontoid) appearance. The mesopterygoid in the London Clay specimen is much larger, and the metapterygoid much smaller (based on the space available for it between the hyomandibular and quadrate), than in the Recent *T. macropterus.* The palatine of the London Clay specimen is as large and strong to support the beak as the condition found in *T. macropterus* and most other tetraodontoids. Because the frontals are absent, the pterosphenoid (on the left side) is relatively clearly seen. The opercle and preopercle are well preserved but unremarkable.

The cleithrum is variously incomplete or not fully exposed at either end, but it was obviously an exceptionally long and sturdy structure, just as in the Recent *T. macropterus.* The cleithrum courses in a gentle arch from behind the level of the top of the opercle to under the level of the quadrate, where it is abraded away on both sides. Presumably this massive cleithrum continued forward to under the level of the dentary, as is uniquely the case in triodontids among the tetraodontiforms. The proximal ends of the two halves of the pelvis are present between the two cleithra under the posteroventral region of the preopercle, but the greater part of the length of the pelvis is broken off at the level of the ventral edges of the cleithra. The presence of a pelvis is unique to *Triodon* and the Eocene eoplectids among the tetraodontoids. In the 103 mm SL specimen of *T. macropterus* the two halves of the pelvis are unfused but in close contact throughout their lengths. In larger specimens of *T. macropterus* the two halves of the pelvis fuse together in much of the posterior region, while the extreme posterior ends of the two halves still remain separate and end in a cartilaginous plug that may represent the remains of a rudimentary fin-ray element (Tyler & Matsuura 1981:65). In the region between the cleithra and preopercle in the London Clay specimen the remains of the hyoid arch are present, with the ceratohyal being especially clear.

Embedded in the matrix of the skull are scattered remains of scales, with a flat basal plate bearing an emarginate ridge with up to six distal points, relatively similar to the scales on the head of the Recent *T. macropterus.*

Our effort to interpret the otic bones of the London Clay specimen has led to the discovery of a posttemporal bone in the 103 mm SL specimen of *T. macropterus.* The posttemporal is present in all Balistoidei (with the possible exception of one species of highly specialized monacanthid; see Tyler & Matsuura 1981:60), and its supposed loss by all Tetraodontoidei was used by Tyler (1980:243) as one of the defining specializations for that suborder. In the two large adult cleared and stained specimens (391 and 463 mm SL) previously examined by Tyler, the area on the dorsal surface of the posterolateral region of the skull where posttemporals might be expected to be found on the basis of their occurrence in the Balistoidei, seemed fully consolidated into a single bone. Thus, the posttemporal was assumed to have been lost phylogenetically or incorporated indistinguishably into the pterotic in *Triodon* and all of the other Tetraodontoidei. However, in the 103 mm SL specimen of *T. macropterus* a large separate posttemporal overlies the dorsal and posterolateral surface of the pterotic. The posttemporal is prominent in both dorsal view, where it forms all of the posterolateral re-

gion of the skull, and in lateral view, where it forms a wedge-shaped buttress for articulation with the head of the supracleithrum. For purposes of clarifying the relationships of the posttemporal and the underlying pterotic, the posttemporal has been detached from the right side of the skull of the 103 mm specimen of *T. macropterus* and so illustrated.

In the London Clay specimen the pterotic is seen mainly on the left side of the skull, as a ventrally produced flange for support of the upper rear edge of the hyomandibular, just as in the Recent species (this flange is broken away on the right side). We believe that the bone just above this flange forming the posterolateral region of the skull in the London Clay specimen is the posttemporal, even though its articulations with the exoccipital medially, epiotic anteriorly, and pterotic ventrally are unclear.

The presence of a posttemporal in *Triodon* is one less way in which the Tetraodontoidei can be distinguished from the Balistoidei and one more way in which triodontids retain primitive balistoid features that have been lost by all other Tetraodontoidei.

Conclusion

The similarity of the distinctive features of the skull and jaws of the Eocene *Triodon antiquus* with those of the Recent *T. macropterus* is assurance of the existence about 50 million years ago of a fish rather like the extant species, and argues for the retention of the fossil and Recent species in the same genus. The Triodontidae, the most primitive family of Tetraodontoidei other than the Eocene eoplectids, has been remarkably conservative in its anatomy since the Eocene, when its lineage separated from that of the other three Recent families of the suborder.

Material

Triodon macropterus Lesson. Australian Museum (AMS) I 25802-006, 1 specimen, 103 mm SL, Queensland; California Academy of Sciences (CAS, specimen formerly at Stanford University (SU)) 13747, 1, 391 mm, Philippines; Academy of Natural Sciences (ANSP) 98917, 1, 463 mm, Japan.

Triodon antiquus Leriche. For materials that are relatively unabraded and intact, the measurement given for the premaxilla is its length and for the dentary is its greatest width across the posterolateral rami. Most materials, however, are severely abraded or fragmented, and the measurement is then the greatest dimension of the piece, which in the case of dentaries is still across the abraded rami if possible. United States National Museum of Natural History (USNM) 265387, 1 dentary, 10 mm, Popes Creek, Charles County, Maryland, Lower Eocene of Pamunkey Group, Nanjemoy Formation, the specimen described by Weems & Horman (1984:47). All of the following are in the British Museum (Natural History) (BM(NH)). From the London Clay Formation (Ypresian): P.62702, skull, 40 mm from front of jaws to rear of supraoccipital, Sheppey, Kent; P.52519, dentary, 10 mm, Sheppey; P.46696, front of dentary, 5 mm, Sheppey; P.28899, tooth-bearing fragment, 7 mm, Bognor Regis, Sussex. From the Wittering Formation (Lutetian): P.50857, tooth-bearing fragment, 7 mm, East Wittering, Sussex. From the Earnley Formation (Lutetian): P.38620, dentary, 11 mm, Southampton, Hampshire; P.22348, dentary, 10 mm, Southampton; P.28190, front of dentary, 7 mm, Southampton; P.51560, dentary, 11 mm, and incomplete right premaxilla, 7 mm, Yateley, Hampshire; P.25776–81, five dentaries, some incomplete, 4–7 mm, and one right premaxilla, 7 mm, Southampton. From the Bracklesham Group (unspecified Formation, Lutetian): P.26426, right premaxilla, 7 mm, Bracklesham Bay, Sussex. From the lower Barton Formation (Bartonian): P.12629, right premaxilla, 8 mm, and two fragments, 4–6 mm, Barton Clay, Barton, Hampshire; P.58456–8, a left premaxilla and two fragments of premaxilla, one left and one right, 6–7 mm,

Bed A3, Barton; P.15193, right premaxilla, 11 mm, and a 6 mm tooth-bearing fragment, Barton; P.14028, front of right premaxilla, 6 mm, lower Barton Clay, Barton. From the Bruxelles Formation (Lutetian): P.15726, front of dentary, 7 mm, Schaerbeek (Kattepoel), Belgium, specimen received from M. Leriche in 1931.

We have no explanation for the fact that of the identifiable disarticulated jaw parts in the BM(NH), all but three of the 14 Ypresian and Lutetian (older) specimens are dentaries, whereas all six of the Bartonian (younger) specimens are premaxillae. Presumably it needs no more explanation than the sampling error that also must be responsible for the fact that seven of the nine identifiable premaxillae are from the right side.

Acknowledgments

We are most grateful to Brian Gasson, Redhill, Surrey, for donating his London Clay *Triodon* skull to the British Museum (Natural History). We thank Richard Winterbottom, Royal Ontario Museum, and G. David Johnson, National Museum of Natural History, for presubmission comments on the manuscript, which was further improved by the reviews of Lance Grande, Field Museum of Natural History, and J. D. Stewart, Los Angeles County Museum of Natural History. John Paxton, Australian Museum, William Eschmeyer, California Academy of Sciences, and Eugenie Böhlke, Academy of Natural Sciences of Philadelphia are thanked for the loan of specimens. At the National Museum of Natural History we appreciate the photography of Chip Clark and the typing of Judy Lombardo and Diane Tyler.

Literature Cited

Burgess, W., & H. R. Axelrod. 1974. Pacific marine fishes. Book 5. Fishes of Taiwan and adjacent waters. T.F.H. Publications, Neptune City, New Jersey, pp. 1111–1381.

Casier, E. 1946. La faune ichthyologique de l'Yprésien de la Belgique.—Mémoires du Musée Royal d'Histoire Naturelle de Belgique 104:1–267.

———. 1960. Note sur la collection des poissons Paléocènes et Eocénes de l'Enclave de Cabinda (Congo).—Annales du Musée Royal du Congo Belge (Tervuren), A (Minéralogie, Géologie, Paléontologie), série 3 (Paléontologie) 1–2:1–47.

———. 1966. Faune ichthyologique du London Clay. British Museum (Natural History), 496 pp.

Dartevelle, E., & E. Casier. 1943. Les poissons fossiles du Bas-Congo et des régions voisines (première partie).—Annales du Musée du Congo Belge (Tervuren), A (Minéralogie, Géologie, Paléontologie), série 3, 2(1):1–200.

———, & ———. 1949. Les poissons fossiles du Bas-Congo et des régions voisines (deuxième partie).—Annales du Musée du Congo Belge (Tervuren), A (Minéralogie, Géologie, Paléontologie), série 3, 2(2):201–256.

———, & ———. 1959. Les poissons fossiles du Bas-Congo et des régions voisines (troisième partie).—Annales du Musée Royal du Congo Belge (Tervuren), A (Minéralogie, Géologie, Paléontologie), série 3, 2(3):257–568.

Gloerfelt-Tarp, T., & P. J. Kailola. 1984. Trawled fishes of southern Indonesia and northwestern Australia. Australian Development Assistance Bureau, 406 pp.

Kyushin, K., K. Amaoka, K. Nakaya, & H. Ida. 1977. Fishes of Indian Ocean. Japan Marine Fishery Resource Research Center, 392 pp.

———, ———, ———, ———, Y. Tanino, & T. Senta. 1982. Fishes of the South China Sea. Japan Marine Fishery Resource Research Center, 333 pp.

Leriche, M. 1905. Les poissons Éocènes de la Belgique.—Mémoires du Musée Royal d'Histoire Naturelle de Belgique 3:49–228.

———. 1906. Contribution a l'étude des poissons fossiles du nord de la France et des régions voisines. Mémoires de la Société Géologique du Nord (Lille) 5:1–430.

———. 1908. Les vertébrés du nummulitique de l'Aude. *In* L. Doncieux, ed., Catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Herault, 2 partie.—Annales de Universite de Lyon, nouvelle série 22:1.

———. 1919. Sur des poissons fossiles de la région côtiére du Congo et sur la présence de l'Eocène dans cette région.—Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences (Paris) 169(10):479–481.

———. 1920. Note préliminaire sur des poissons nouveaux du Paléocène et de l'Éocène de la région côtière du Congo.—Revue Zoologique Africaine (Bruxelles) 8:80–86.

Matsuura, K. 1985. *Triodon macropterus* Lesson. P. 748 *in* O. Okamura, ed., Fishes of the Okinawa Trough and the adjacent waters. Japan Fisheries Resource Conservation Association, 781 pp.

Nolf, D. 1970. De geremanieerde Eocene visfauna in de basis van het Pleistoceen te Merelbeke.—Natuurwetenschappelijk Tijdschrift (Gent) 51(3–8):111–124.

Smith, M. M. 1986. Triodontidae. P. 894 *in* M. M. Smith, & P. C. Heemstra, eds., Smith's sea fishes. Macmillan South Africa, Johannesburg, 1047 pp.

Taverne, L., & D. Nolf. 1978. Troisième note sur les poissons des Sables de Lede (Eocène Belge): les fossiles autres que les otolithes.—Bulletin de la Société Belge de Géologie 87(3):125–152.

Tyler, J. C. 1962. *Triodon bursarius,* a plectognath fish connecting the Sclerodermi and Gymnodontes.—Copeia 1962(4):793–801.

———. 1967. A redescription of *Triodon macropterus* Lesson, a phyletically important plectognath fish.—Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, series C 70(1):84–96.

———. 1980. Osteology, phylogeny, and higher classification of the fishes of the Order Plectognathi (Tetraodontiformes).—National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service Circular 434: 1–422.

———, & K. Matsuura. 1981. Comments on the osteology of balistoid fishes (Tetraodontiformes) with notes on the triodontid pelvis.—Proceedings of the Biological Society of Washington 94: 38–49.

Weems, R. E., & S. R. Horman. 1983. Teleost fish remains (Osteoglossidae, Blochiidae, Scombridae, Triodontidae, Diodontidae) from the lower Eocene Nanjemoy Formation of Maryland.—Proceedings of the Biological Society of Washington 96:38–49.

Winterbottom, R. 1974. The familial phylogeny of the Tetraodontiformes (Acanthopterygii: Pisces) as evidenced by their comparative myology.—Smithsonian Contributions to Zoology 155:1–201.

(JCT) Office of the Director, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.; (CP) Department of Paleontology, British Museum (Natural History), London SW7 5BD, England.

PROC. BIOL. SOC. WASH.
104(4), 1991, pp. 892–893

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

% The Natural History Museum
Cromwell Road
London, SW7 5BD, U.K.

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 27 June 1991 in Vol. 48, Part 2 of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD.

Case No.

2729 *Fusus* Helbling, 1779 (Mollusca, Gastropoda): proposed confirmation of unavailability.

2753 *Cycloceras* M'Coy, 1844 (Mollusca, Nautiloidea): proposed designation of *C. laevigatum* M'Coy, 1844 as the type species, and proposed designation of a neotype for *C. laevigatum.*

2765 *Phyllodoce* Lamarck, 1818 and *Polyodontes* de Blainville, 1828 (Annelida, Polychaeta): proposed conservation.

2791 *Chelifer museorum* Leach, 1817 (currently *Cheiridium museorum*; Arachnida, Pseudoscorpionida): proposed conservation of the specific name.

2759 *Goniosoma conspersum* Perty, December 1833 (currently *Mitobates conspersus*; Arachnida, Opiliones): proposed conservation of the specific name.

2292 Histoire abrégée des insectes qui se trouvent aux environs de Paris (Geoffroy, 1762): proposed conservation of some generic names (Crustacea and Insecta).

2757 *Rhinapion* Beguin-Billecocq, 1905 (Insecta, Coleoptera): proposed conservation.

2737 *Brahmaea* Walker, 1855 (Insecta, Lepidoptera): proposed confirmation of *Bombyx certhia* Fabricius, 1793 as the type species.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 27 June 1991 in Vol. 48, Part 2 of the *Bulletin of Zoological Nomenclature.*

Opinion 1635. *Gryphaea pitcheri* Morton, 1834 (currently *Texigryphaea pitcheri*; Mollusca, Bivalvia): specific name conserved.

Opinion 1636. *Myriochele* Malmgren, 1867 and *Myriochele oculata* Zaks, 1923 (Annelida, Polychaeta): conserved.

Opinion 1637. *Aphonopelma* Pocock, 1901 (Arachnida, Araneae): given precedence over *Rhechostica* Simon, 1892.

Opinion 1638. *Holostaspis subbadius* var. *robustulus* Berlese, 1904 (currently *Macrocheles robustulus*; Arachnida, Acarina): specific name conserved.

Opinion 1639. *Shoemakerella* Pirlot, 1936 (Crustacea, Amphipoda): *Lysianax cubensis* Stebbing, 1897 designated as the type species.

Opinion 1640. *Ranguna* Bott, 1966 and *Larnaudia* Bott, 1966 (Crustacea, Decapoda): *Potamon rangoonensis* Rathbun, 1904 and *Thelphusa larnaudii* A. Milne Edwards, 1869 confirmed as the respective type species.

Opinion 1641. *Carcinochelis* Fieber, 1861 (Insecta, Heteroptera): *Carcinochelis alutaceus* Handlirsch, 1897 designated as the type species.

Opinion 1642. *Chlorophanus* Sahlberg, 1823 (Insecta, Coleoptera): conserved.

Opinion 1643. *Ceratopogon puncticollis* Becker, 1903 (currently *Culicoides puncticollis*; Insecta, Diptera): given precedence over *Ceratopogon algecirensis* Strobl, 1900.

Opinion 1644. *Culex stigmatosoma* Dyar, 1907 and *C. thriambus* Dyar, 1921 (Insecta, Diptera): specific names conserved.

Opinion 1645. *Musca heraclei* Linnaeus, 1758 (currently *Euleia heraclei*; Insecta, Diptera): specific name conserved.

Opinion 1646. *Coccobius* Ratzeburg, 1852 (Insecta, Hymenoptera): not suppressed.

Opinion 1647. *Heteronota pelagica* Girard, 1857 (currently *Gymnodactylus, Cyrtodactylus* or *Nactus pelagicus*; Reptilia, Sauria): given precedence over *Gymnodactylus arnouxii* Duméril, 1851.

Opinion 1648. *Micropterus patachonicus* King, 1831 and *Anas pteneres* Forster, 1844 (both currently in *Tachyeres* Owen, 1875; Aves, Anseriformes): specific names conserved.

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON" a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Apendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

Proofs.—Authors will receive first proofs and original manuscript for correction and approval. Both must be returned within 48 hours to the Editor. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, **changes in proofs ($3.00 per change or revision),** and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. If subsidized manuscripts result in more than 12 printed pages, the additional pages must be financed by the author(s). Multiple authorship will not alter the 12 page limit (each author will be viewed as having used his/her 12 subsidized pages). Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch. One ms. page = approximately 0.4 printed page.

CONTENTS

Preliminary phylogenetic systematic analysis of the major lineages of the Eucestoda (Platyhelminthes: Cercomeria) Daniel R. Brooks, Eric P. Hoberg, and Peter J. Weekes 651

New hydrobiid snails (Mollusca: Gastropoda: Prosobranchia: Truncatelloidea) from North America Fred G. Thompson and Robert Hershler 669

Redescription of *Helmetophorus rankini* Hartman, 1978 (Polychaeta: Helmetophoridae) and its transfer to the Flabelligeridae Christopher J. Glasby and Kristian Fauchald 684

Polynoids commensal with gorgonian and stylasterid corals, with a new genus, new combinations, and new species (Polychaeta: Polynoidae: Polynoinae) Marian H. Pettibone 688

Polynoid polychaetes commensal with antipatharian corals Marian H. Pettibone 714

Lepeophtheirus spatha, a new species of copepod (Siphonostomatoida: Caligidae) parasitic on the California halibut from Santa Monica Bay, California Masahiro Dojiri and Robert A. Brantley 727

The Stillman Wright collection of Copepoda (Crustacea) from South America in the National Museum of Natural History, Smithsonian Institution Janet W. Reid 736

V. L. Wagin's collections of Dendrogastridae (Crustacea: Ascothoracida) in the U.S.S.R., with designations of lectotypes Mark J. Grygier 742

Rediagnosis and revision of some Nannastacidae (Crustacea: Cumacea) Les Watling 751

Synisoma wetzerae, a new species and the first record of *Synisoma* from the New World (Crustacea: Isopoda: Valvifera: Idoteidae) Bernard Ormsby 758

Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea) Raymond B. Manning and Darryl L. Felder 764

A new hermit crab (Decapoda: Paguridae) from rocky shores of the Ogasawara (Bonin) Islands Akira Asakura 793

A new generic assignment for a South American Crayfish (Decapoda: Parastacidae) with revised diagnoses of the South American genera and comments on the parastacid mandible Horton H. Hobbs, Jr. 800

Pandalus gurneyi Stimpson synonymized with *Pandalus danae* Stimpson (Decapoda: Pandalidae) Mary K. Wicksten 812

S. W. Williston's species of Ephydridae (Diptera) from St. Vincent (West Indies) Wayne N. Mathis and James F. Edmiston 816

Exallodontus aguanai, a new genus and species of Pimelodidae (Pisces Siluriformes) from deep river channels of South America, and delimitation of the subfamily Pimelodinae John G. Lundberg, Francisco Mago-Leccia, and Pedro Nass 840

The identity and taxonomic status of *Megapodius stairi* and *M. burnabyi* (Aves: Megapodiidae) David W. Steadman 870

The skull of the Eocene *Tridon antiquus* (Triodontidae: Tetraodontiformes): similar to that of the Recent threetooth pufferfish *T. macropterus* James C. Tyler and Colin Patterson 878

International Commission on Zoological Nomenclature 892

Table of Contents, Volume 104 895

Index to New Taxa, Volume 104 898

SMITHSONIAN INSTITUTION LIBRARIES

SMITHSONIAN INSTITUTION LIBRARIES

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 01205 2296